THE
AMERICAN NATURALIST

VOL. LIV. *November–December, 1920* NO. 635

TYPES OF WHITE SPOTTING IN MICE[1]

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THE occurrence of white spotting in the coats of colored mammals is one of the commonest phenomena encountered by the student of variation and heredity. For a long time spotting was thought to be of the same nature as albinism, a condition in which no pigment is present in the fur and eyes, leaving the pelage clear white and the eyes pink. Many specimens of white spotted animals are still to be seen in museums masquerading as "partial albinos."

As soon as the methods of experimental breeding were employed in studying such variations, albinism and white spotting were found to be genetically distinct. Albinism, because of the striking nature of the variation and its almost identical appearance wherever encountered was one of the first mammalian variations to be analyzed and its mode of inheritance is now well known. The case of white spotting is quite different. The spotting of most animals presents an extremely wide range of variation. An almost continuous series may be traced by the casual observer from the extreme spotting of white dogs with black eyes to the small star or blaze on the foreheads of some colored horses. The solid colored condition, generally known as self, and spotting may thus in some instances be distinguished only by the presence of a few white hairs. Moreover, the inheritance of white spotting in different animals and of the various grades of

[1] The experiments reported in this paper were performed at the Bussey Institution, Harvard University, Forest Hills, Mass.

spotting in the same animal has been found by experiment to be distinctly different. Our knowledge of the hereditary factors and of the processes concerned with the development of pigment in the coat is still too fragmentary for a satisfactory comparative exposition of the nature and causes of white spotting. The need at present appears rather to be for intensive experimental studies of variations in the most favorable species in which they occur. The white spotting of some species also provides excellent material for the study of the nature of genes with small quantitative effects either as main or as modifying factors. As a contribution to these ends the present report of experiments with white spotting in mice is offered.

In the house mouse the whole range of variability in white spotting is found. At one extreme are black-eyed whites, with pigment occurring only in the eyes; at the other extremes are colored mice which have only a few white hairs on forehead, feet, tail or belly. The appearance of all possible intergrades between black-eyed whites at one end of the scale and animals closely resembling self at the other led Cuenot to suppose that all spotted mice differed from self by a single main spotting factor (P) which might be present in various conditions represented by factors with minor effects which caused the more apparent differences in amount of pigmented areas. The finer details and intergrades of spotting he regarded as purely somatic variations with no germinal (hereditary) cause. Later, however, Little (1915) bred spotted mice and classified all parents and offspring by estimating the percentage relations between white and colored spaces. He found that the "continuous" series of spotted forms consisted of two main types. One of these, black-eyed white, was characterized by a pelage practically all white with dark eyes. The other, piebald, was distinguished by the greater extent of pigmented areas down to and including mice with only a few white hairs dorsally and a small patch of white on the belly. Another type of spotted mouse known as "blaze" and

characterized only by a small white spot between the eyes was also removed from the continuous series by the work of Little (1917). This variation was apparently heritable, although subect to some variability in expression. Two types of piebald spotting, one with more and one with less white were likewise indicated in Little's data. He regarded these differences as possibly due to two distinct modifying factors of the piebald gene. In addition, crosses of black-eyed white with self-colored mice had produced two new spotted types, one with more and one with less white. The continuous series of spotted forms has thus been broken up on the basis of amount and distribution of spotting into a large number of fairly distinct types, two of them due to genes the inheritance of which is known. The process of resolution has not reached its end yet, for a great deal of variability exists within the various types, and the resolution of these variations into still more sub-types is possible. The specific objects of this study are to redefine the ranges of the main types of spotting in the light of increased data; (2) to find out, if possible, whether the conditions of spotting in the sub-types are due to different combinations of the main genes or to distinct genes which modify the expression of the main genes.

The two main types of spotting in mice are known respectively as black-eyed white and piebald. Little at first described black-eyed whites as spotted mice which were 95 per cent. or more white dorsally, later extending this limit to include mice which are 80 per cent. or more white dorsally. Certain yellow black-eyed whites were described by Little (1917) as exhibiting as little as 60 per cent. of white in the dorsal surface. Evidence will be presented later to show that the range of black-eyed white variability is even greater than this and may include mice with as little as 50 per cent. of dorsal white.

Piebalds are much darker, *i.e.*, have less white spotting than black-eyed whites. The piebalds born in my experiments have, with one or two exceptions, been less than 50 per cent. white dorsally with belly spotting rang-

ing from 12 per cent. to 85 per cent. of white. Other investigators have recorded piebalds whiter than this[2] and one or two of my crosses indicate that piebalds may exhibit as much as 60 per cent. or 65 per cent. white, although such animals have been extremely rare in these experiments.

Genetically these two types of spotting are distinct, and each is due to a gene distinct from and independent of the other. When black-eyed whites are crossed with piebalds equal numbers of black-eyed whites and piebalds result. When black-eyed whites are bred *inter se,* black-eyed whites and piebalds result in the ratio of 2:1. The black-eyed white condition is therefore due to a gene (symbol *W*) acting with the gene for piebald (symbol *s*). Black-eyed whites are heterozygous for the gene *W* and are homozygous for *s*. Genetically they are *Wwss*. Piebalds may be represented by the formula *wwss,* where *w* stands merely for "not-black-eyed white." These two genes, as is known from previous data (Little, 1915; Dunn, 1920), are neither allelomorphic nor linked, but entirely independent.

As additional evidence of the distinctness of these types and to illustrate the comparative ranges as regards amount of white spotting on the dorsal surface, the data from a number of crosses between black-eyed whites and piebalds are presented in Table II, Cross 1, and Fig. 1 solid line. All mice in this as in other distributions to be discussed were graded by estimating the amount of white in the coat. The two surfaces, dorsal and ventral, were graded separately, the total of each surface being regarded as 100. The percentage of dorsal white was expressed as the numerator and the percentage of ventral white as the denominator of a fraction. Thus a mouse entirely white dorsally and ventrally (except for pigment in the eyes) was graded as 100/100; while one with only a small patch of white ventrally was

[2] For instance, the race of pure Japanese piebalds described by Little (1917) which varied from 100 per cent. to 64 per cent. white dorsally and closely resembled black-eyed whites in amount of spotting.

graded 0/1, or 0/3, etc. The results can be easily transposed into Little's scale by simple subtraction of any grade from 100, since his percentage expressed the amount of color. For convenience, only the dorsal grades have been used in the tabulation, since the results

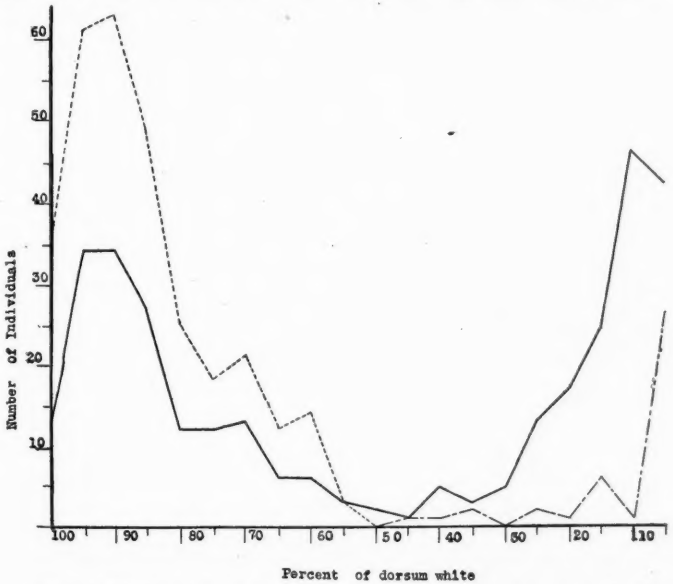

FIG. 1. Showing graphically the distribution as regards amount of white spotting of (1) all black-eyed white mice (dotted line); (2) offspring of crosses of black-eyed white by piebald (solid line); (3) offspring of cross of black-eyed white by self (broken line).

obtained by using the ventral grades are in all respects similar.

Of 323 mice raised from crosses of black-eyed whites by piebalds, approximately half (160) were 50 per cent. white or more; the other half (163) were spotted mice with less than 50 per cent. white; expected 161.5 of each. No mice were obtained early in the experiment which were from 55 to 51 per cent. white and it was thought that this zero class indicated a clear discontinuity between the types. With larger numbers, however, three mice of this sort were born. That the division between black-eyed white and piebald at 51 per cent. is, however,

not an arbitrary one is shown by the bimodal nature of the curve (Fig. 1, solid line), which divides itself near 50 per cent.; by the closeness with which the actual assortment of *W* and *w* (assuming the lower limit of *W* spotting as 51 per cent.) approaches the expected and by breeding tests of spotted mice slightly more and slightly less than 50 per cent. white. Those more than 50 per cent. white proved to be black-eyed white and those less than 50 per cent. white proved to be piebalds.

The mode of the black-eyed whites in this distribution is at 95–86 per cent. white, although when all other black-eyed whites are added (Table II, Cross 8, Fig. 1, broken line) the main mode is found to be at 90–86. The range is from 100 per cent. to 51 per cent. and the mean of all black-eyed whites is 83.5 per cent. $\pm$ .4 with a standard deviation of 11.4 per cent. $\pm$ .3.

This establishes a wider range of variability for the black-eyed white variation than has been current heretofore, by the addition to the distribution of the classes less than 80 per cent. white. It will be shown later in the section on modifying factors that these darker classes are not merely somatic fluctuations in the expression of the gene for black-eyed white (*W*) but represent genetic variations. They may be regarded as sub-types of black-eyed white.

PIEBALD

The piebalds produced by the cross of black-eyed white with piebald are represented by that part of the solid line (Fig. 1) lying between 50 per cent. and 0 per cent. Unlike black-eyed whites, piebalds are not always distinguishable on the basis of dorsal white alone, for some piebalds have no white at all dorsally. In such cases the ventral white must be used as a criterion, and of the pure piebalds produced in this cross none had less than 12 per cent. of ventral white and this was used as the limit of piebald variability. All animals with 12 per cent. or more of ventral white and with from 0 to 5 per cent. of dorsal white were placed in the 0–5 per cent. class. The correctness of this classification can be inferred from the

closeness with which the numbers of piebalds resulting from various crosses (Table II) agree with the numbers expected on the assumption that the gene *s* segregates at random with regard to *S*, *W*, and *w*. It is certain,

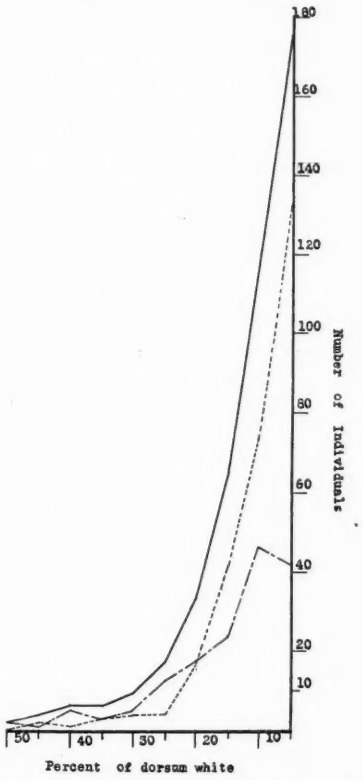

FIG. 2. Showing graphically the distribution as regards amount of white spotting of (1) all piebald mice (solid line); (2) piebald mice resulting in the second generation from a cross of piebald by self (dotted line); (3) piebalds extracted from black-eyed whites (broken line).

nevertheless, that all possible variations of piebald have not been met with in the distributions presented in Table II and Fig. 2. Little (1917) bred a race of pure piebalds which varied from 100 per cent. to 64 per cent. white dorsally. These piebalds are entirely outside the range of the piebalds bred in the present experiments. Moreover,

since the conclusion of these experiments I have been able to isolate one family of piebalds characterized by from 0–10 per cent. of white dorsally and from 0–12 per cent. of white ventrally. They have even produced a small proportion of solid colored young which probably represents an extreme condition of piebald in connection with other subsidiary factors for the increase of pigmented areas. Thus aside from the piebald mice observed in these experiments it can be seen that the genotype "*ss*" (piebald) may vary somatically from solid colored to all white with dark eyes.

As regards only the piebalds observed in this investigation (and this includes all the piebalds in the experiment, 437 in number) it can be seen by a glance at Table II, Cross 11, and Fig. 2 that they constitute a well-defined class ranging from 50 per cent. to 0 per cent. white dorsally. Of the total (437) 295, or 67 per cent., are less than 10 per cent. white. They are less variable than the black-eyed whites, since the standard deviation of 302 black-eyed whites is $11.4 \pm .3$, while the standard deviation of 437 piebalds is $8.6 \pm .2$. This difference is not due to the range which is 50 per cent. in each case, but to the grouping of the piebalds in the two darkest classes while the black-eyed whites are distributed more evenly throughout the distribution. The mean and standard deviation of piebalds out of crosses with self (Table II, Cross 10) are significantly lower than the same constants from piebalds out of crosses with black-eyed white. An interpretation of these differences is offered below in the section on modifying factors.

The main difference between the black-eyed white and piebald condition is due to the presence in the black-eyed whites of a dominant gene (*W*) which the piebalds lack. This gene in single dose, and in connection with the gene for piebald, limits the formation of pigment to, on the average, about 10 per cent. of the dorsal surface, though mice possessing this combination of genes may vary from all white with dark eyes to about 50 per cent. white.

The piebald gene in double dose and acting alone per-

mits the formation of pigment on the average, in about 85 per cent of the dorsal surface, although such mice may vary from solid colored dorsally (0 per cent. white) to 100 per cent. white dorsally.

There are certain other combinations of these genes possible, and by experiment these other combinations have been found to produce other spotted types. Some of these types have been found to be indistinguishable somatically from piebald, although differing from piebald in genetic constitution. The experimental evidence bearing on the appearance, constitution and variability of such additional types follows.

Type "A" Spotting

When black-eyed white is crossed with self approximately half of the progeny are spotted and half are self or exhibit at most only a small white ventral spot. From such a cross in the present experiments 76 young have been born, of which 40 were spotted and 36 were self colored (Table II, Cross 2). Little found that the self (or nearly self) young from such a cross were ordinary heterozygotes between self and piebald. The spotted young he found to be due to unions of gametes carrying black-eyed white and piebald (*Ws*) with self gametes (*wS*) producing the double heterozygote *WwSs*. He called such spotted mice Type "A". The somatic expression of this combination of genes has produced spotted mice varying from 0 to 45 per cent. of white dorsally (Fig. 1, broken line, and Fig. 3, dotted line). The distribution as regards amount of white dorsally is seen from this figure to resemble closely the distribution of piebald in range, while the mode of Type "A" is at 5–0 per cent. and the mode of all piebalds is at the same point. The mean of all Type "A"s raised (83 in number) was $7.9 \pm .6$ per cent. white dorsally with a standard deviation of $8.4 \pm .4$. This is very close to the mean of all piebalds (9.7 per cent. white) and almost identical with the mean of piebalds extracted from crosses of piebalds with self ($8.05 \pm .3$). Moreover, Type "A"s which have

no dorsal white may be characterized by an extremely small amount of ventral white. Ordinarily mice with less than 12 per cent. of ventral white may be classed as self. I mated together two such apparently self animals out of a cross of Type "A" by piebald. Each had a small white spot on the belly only covering 4 per cent. of that surface in one of the mice and 5 per cent. in the other. They produced two litters, each of which contained two black-eyed white mice. They were Type "A" mice and not selfs as they had been recorded. A similar case has been reported by Little (1917) in which eleven yellow mice with 6 per cent. and more of ventral spotting proved on breeding tests to be Type "A". That an extreme of Type "A" spotting approached the self condition so closely was not discovered until most of the animals had been graded. It is possible, therefore, that where Type "A" and self animals appear in the same distribution, the self class may be factitiously enlarged at the expense of the Type "A" class, due to errors in grading. Type "A" spotted mice are hence indistinguishable somatically from piebalds, and in certain cases, from selfs, although possessing a genetic constitution entirely different from either of these latter forms.

TYPE "C"

There remains one other type of spotting to be discussed which like Type "A" and piebald has a different genetic constitution, but which is difficult to distinguish from either Type "A" or piebald. Such mice are produced when Type "A" animals are interbred. Each Type "A" produces gametes *WS, Ws, wS* and *ws* which by random union give the following array of zygotes:

4 pure for *W* which are non-viable and die in utero.
4 *WwSs*—Type "A"
2 *wwSs* } self
1 *wwSS* }
2 *Wwss*—black-eyed white
2 *WwSS*—dark spotted (Type "C")

$\frac{1}{16}$ *wwss*—piebald

The visible distribution should consist of approximately 2 black-eyed whites, 7 spotted, and 3 self. The experimental numbers for this cross (Table I, Cross 4) in the present study are 16 black-eyed whites, 27 "spotted,"[3] and 18 selfs. Among the spotted forms is included a new genotypic class consisting of mice which are heterozygous for *W* but pure for self. Little called this genotype "dark spotted," but since somatically it is no darker than other spotted types I shall refer to it arbitrarily as Type "C." Some of the spotted mice from the above cross (4) were tested by crossing them with piebalds. If the mouse tested were piebald, it should produce only spotted (piebald) mice; if it were Type "A" it should produce black-eyed whites, spotted and selfs; while if it were Type "C" it should produce only spotted (Type "A") and self. Out of a number of mice so tested only seven proved to be Type "C" and the only evidence available on the appearance of Type "C" mice is from the appearance of these tested animals. Five were less than 5 per cent. white dorsally; one was 7 per cent. white and one was 8 per cent. The white spotting in all of them was confined to the head, either as a spot on the nose or between the eyes ("blaze"). It is to be regretted that no animals from this cross with less than 12 per cent. of ventral white were tested, since it seems probable from the excess of selfs recorded that some mice graded as self and were really Type "C." The same excess of selfs was noted in a larger amount of data on this cross reported by Little. Its significance is probably the same, that is, it is due to the production of an extremely small amount of spotting by the genetic Types "A" and "C."

Crosses of Type "C" with piebald produced a total of 85 offspring (Table II, Cross 6), of which 43 were spotted and 42 were self (expected 42.5 of each). The spotted

[3] Under the general term "spotted" are included all those genotypes which are somatically indistinguishable when occurring in the same distribution, viz., Type "A," Type "C," and piebald.

mice were genetically Type "A" (*WwSs*) and their distribution is shown graphically in Fig. 3, broken line. This distribution resembles that of the Type "A"s produced by crossing black-eyed white with self, except that the former are somewhat less variable, due to the ab-

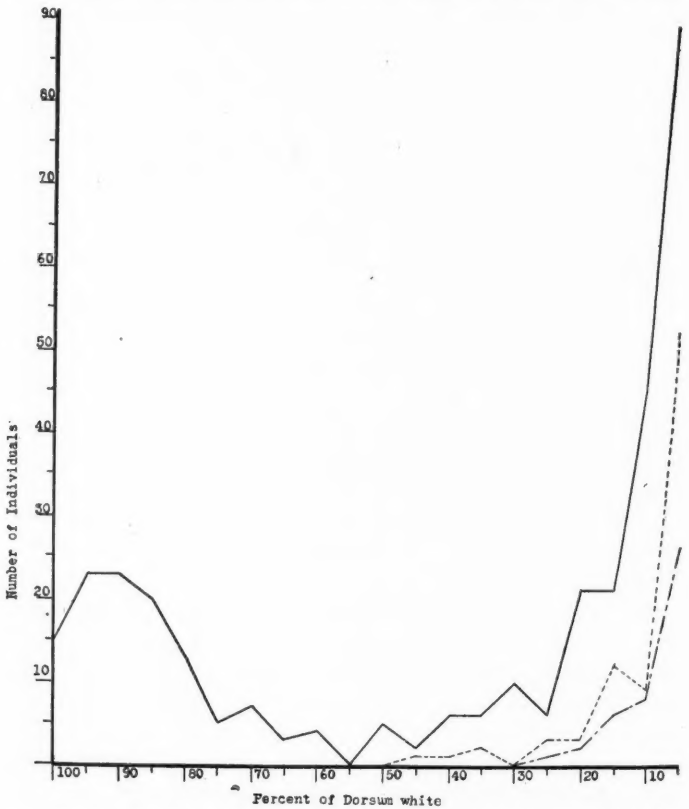

FIG. 3. Showing graphically the distribution as regards amount of white spotting of (1) offspring from crosses of Type A by piebald (solid line); (2) of all Type A mice (dotted line); (3) offspring of crosses of Type C by piebald (broken line).

sence of classes lighter than 25 per cent. white, and their mean is somewhat lower for the same reason. These differences are probably due to the selection of dark Type "C"s as parents and it will be seen later that the darker

spotted types probably carry modifying genes which have a pronounced effect in increasing the amount of pigment present.

Many crosses were made between Type "A" and piebalds with the object of determining whether the genes *W* and *s* were linked or independent. All offspring from this cross were also graded for variation in amount of white spotting. The distribution of the 443 offspring (Table II, Cross, and Fig. 3 solid line) indicates the correctness of the ranges already established for three types of spotting, since black-eyed whites, "spotted" (Type "A" and piebald) and selfs resulted in the expected ratio of 1:2:1. The range of the black-eyed whites was from 100 to 56 per cent. white; and "spotted" from 50 to 0 per cent. white. The mean of the black-eyed whites was 84.7 per cent. ± .6 of white dorsally with a standard deviation of 10.3 ± .5, which values correspond closely to those calculated for the cross black-eyed white × piebald (Table II, Cross 1). The mean of the mixed spotted was at 11.6 per cent. ± .5 compared with 12.5 per cent. ± .6, the mean of the piebalds in Cross 1. It may be inferred from this that the residence in the same Type "A" zygote of the genes *W* and self has had *per se* no darkening effect on the black-eyed whites and spotted subsequently extracted.

Self

Data on the ranges of variability of white spotted mice would not be complete without some reference to the variability exhibited by mice which by all tests which have been applied to them are genetically self mice, *i.e.*, lacking the genes at present known to cause white spotting. The heterozygote between self and piebald is generally regarded as self, that is, self is supposed to be completely dominant to piebald. But in a number of cases in these experiments heterozygotes between self and piebald have exhibited a small spot of white on the belly, covering never more than 12 per cent. of the ventral surface. This occurrence has been remarked by Little in the case of Type "B" mice resulting from the

cross black-eyed white by self. Further reference will be made to these mice in the section on modifying factors. In addition certain mice have appeared which exhibit only a small white spot in the form of a "blaze" of white hairs between the eyes which may or may not be accompanied by a small belly spot. Such mice have proved to be self in distinction from piebald since when mated *inter se* they have produced 15 self-colored mice lacking any spotting and 6 piebalds, indicating that both "blaze" parents were selfs heterozygous for piebald. When tested by crossing with pure piebalds, such "blaze" mice have produced 55 selfs and 39 piebalds. Certain of the selfs had a small white spot (always less than 10 per cent.) *ventrally,* and it is possible that these may be piebalds. If so, the ratio of 1 self:1 piebald may be more closely approached, indicating that the small white dorsal spot is a non-genetic imperfection of dominance occurring in self mice heterozygous for piebald. None of the "self" progeny from crosses of blaze with piebald exhibit any dorsal spotting. One other possibility is that the blaze may be due to a separate gene either identical with or similar to the gene which differentiated the blaze mice reported by Little. The second or other segregating generation which is critical for determining this point has not been bred. Of course the term self should apply properly only to mice which show no trace of white spotting. Genetically it is the sum of the factors producing the normal solid coat of the wild mouse and as such should be always the same unless new mutations take place or unless certain somatic variability exists unconnected with a germinal cause. Sufficient data in the case of the dorsal spotting of apparently self mice are not at present available to decide between these alternatives. In the case of the small belly spotting, as will be seen later, the case is somewhat different.

For convenience in reference the range of variability of each of the several genotypes discussed above has been placed in tabular form (Table I). All ranges except that for piebald (line 3) have been drawn from ob-

servations by the writer and all data in the tables and figures of this report have been tabulated according to these ranges. Such a table is approximate and may be only temporary, for the breeding of larger numbers of

SUMMARY OF RANGE DATA

TABLE I

Type of Spotting	Genotype	Per Cent. of Dorsal White	Per Cent. of Ventral White
1. Black-eyed white	*Wwss*	100 to 50	100 to 85
2. Piebald (present series)	*wwss*	50 to 0	85 to 12
3. Piebald (other data)	*wwss*	100 to 0	85 to 0
4. Type A	*WwSs*	45 to 0	90 to 4
5. Type C	*WwSS*	8 to 0	50 to 15
6. Self	*wwSS* or *wwSs*	3 to 0	12 to 0

spotted mice may increase the range now attributed to each type. Whether the ranges of variability represent the norm for each type is not at present known, nor can it be known until each type by inbreeding or other suitable methods has been separated from the subsidiary factors which, as it will appear, alter the expression of the main spotting factors.

MODIFYING FACTORS

The general result of the foregoing discussion is simply an exposition of the great amount of variability existent within each type of spotted mice, all of which are identical as regards the main genes now known to determine white spotting. The question naturally arises, if a mouse with a coat entirely white except for pigment in the eyes and a mouse in which the dorsal surface is equally divided between pigmented and white spaces are genetically identical as regards the main genes *W* and *s*, how then do they differ? Is each merely a somatic variation (fluctuation) of a genetic complex determining a combination of colored and white spaces halfway between these extremes? Or do other genetic factors in combination with the main spotting genes determine greater or less amounts of pigment in the coat?

If we adopt the fluctuation hypothesis then we must

demonstrate that the amount of spotting in the offspring is not correlated with the amount of spotting in the parents. Being due to non-genetic causes, the variations within the type should appear purely at random. An excellent example of this kind of variation has been communicated in a paper read before the American Society of Naturalists at their December, 1919, meeting by Dr. Sewall Wright. The piebald pattern of guinea pigs appeared in his experiments to be determined primarily by one recessive Mendelian gene, the expression of which is altered through extremely wide ranges by environment, sex and the uncontrolled vagaries of development.

The second explanation presumes the occurrence of modifying genes separable in heredity from other genes for spotting, yet only coming to expression in the presence of the main gene or genes for spotting. If this be true, the various grades of spotting within any type such as black-eyed white should be heritable. The amount of spotting in the offspring should be definitely correlated with the amount of spotting in the parents. Whiter black-eyed whites, for example, should have whiter offspring; and darker black-eyed whites should have darker offspring. Little has found some evidence that this may be true of certain grades of piebald, for he noted that the offspring of hybrids between selfs and piebald tended to cluster about the mode of the particular piebald grandparents.

The experimental test of these diverse explanations has in the present experiments consisted of crossing mice of one spotted type with lighter (much spotted) and darker (little spotted) mice of another type. The offspring of the lighter and darker matings have then been compared as to mean and range. Some matings of lighter types *inter se* and darker types *inter se* have been made, and while these have not yet yielded enough offspring to have a decisive bearing on the question, they indicate that black-eyed white and piebalds with more white spotting than the mean of their respective types and with amounts of spotting below the mean

breed fairly true to these different conditions. The results of the first mentioned matings have shown in general that the altered expression of the spotting factors *W* and *s* in the direction of more or less white spotting is definitely transmitted to the offspring. The evidence on this point is presented in Table II.

Cross 1 of this table presents the distribution of offspring of crosses of black-eyed whites with dark piebalds, viz., those with dorsal white spotting ranging from 0–10 per cent. Among the black-eyed white parents all grades of spotting were approximately equally represented. The mode of the black-eyed white offspring is at 85–81 per cent. of white, the mean of white spotting is 80.5 per cent. $\pm$ .7 per cent., and they range from 100 to 51 per cent. white, with a standard deviation of 11.65 $\pm$ .5. The piebald young have a mean grade of 10.9 $\pm$ .4 per cent., a standard deviation of 8.1 $\pm$ 3, and all grades of piebald from 0 to 50 per cent. white are represented, although the majority is less than 20 per cent. white. With these crosses are to be compared the offspring of Cross 2, of which the parents were black-eyed whites of the same grades as were used in Cross 1, and *light* piebalds, viz., those which were more than 10 per cent. white dorsally. The black-eyed white young were centered about a mode at 95–91 per cent. white; their mean is 88.5 per cent. $\pm$ .8 per cent., and their standard deviation 7.8 $\pm$ .5. Their range is considerably less than the range of black-eyed whites in cross 1, due to the absence from the distribution of all classes less than 70–66 per cent. white. The piebald young from Cross 2 have a mean of 16.4 $\pm$ 1.2 per cent. white and a standard deviation of 12.1 $\pm$ .8. The range of the piebalds is the same as in Cross 1, but the lighter classes are more heavily represented than in Cross 1, and this is reflected in the higher standard deviation.

These crosses are a test of the nature of the differences between darker and lighter piebalds. That such differences are genetic is clearly shown by the results, for the lighter piebalds have appreciably lighter offspring

TABLE II

CROSSES OF SPOTTED MICE SHOWING VARIATION IN AMOUNT OF WHITE SPOTTING

Cross	Per Cent. of Dorsal White on Young																				Self	Total
	Black-eyed Whites										Piebald, Type "A," and "Spotted"											
	100–96	95–91	90–86	85–81	80–76	75–71	70–66	65–61	60–56	55–51	50–46	45–41	40–36	35–31	30–26	25–21	20–16	15–11	10–6	5–0		
1. Black-eyed-white × piebald (*Wwss* × *wwss*)	13	34	34	27	12	12	13	6	6	3	2	1	5	3	5	13	17	24	46	42	0	323[7]
2. Black-eyed white × self (*Wwss* × *wwSS*)												1	1	2	0	2	1	6	1	26	36	76
3. Type A × piebald (*WwSs* × *wwss*)	15	23	23	20	13	5	7	3	4	0	5	2	6	6	10	6	21	21	45	89	116	443[8]
4. Type A × Type A (*WwSs* × *WwSs*)	7	3	3					1	2		2		3	1	2	1		1	6	11	18	61
5. Type A × self (*WwSs* × *wwSS*)																		2	13	12	33	60
6. Type C × piebald (*WwSS* × *wwss*)																1	2	6	8	26	42	85
7. Black-eyed white × black-eyed white (*Wwss* × *Wwss*)	1	1	3	2		1	1	2	2				1				1		1	1		17
8. All black-eyed whites (*Wwss*)	36	61	63	49	25	18	21	12	14	3												302
9. All Type "A" (*WwSs*)												1	1	2	0	3	3	12	9	52		83
10. F_2 piebalds from cross of piebald self × (*wwss*)												2	1	3	4	4	16	41	74	133		278
11. All piebalds[9] (*wwss*)											2	4	6	6	9	17	33	65	120	175		437

[6] In this class are placed mice of Types A and C as well as piebalds occurring in the same distribution since these types are not distinguishable somatically.

[7] Includes 5 piebalds not graded.

[8] Includes 3 "spotted" not graded.

[9] Includes all piebalds from Cross 1, from other matings of piebald × piebald, and of F_2 out of piebald × self.

TABLE II.—*Continued*

CROSSES OF SPOTTED MICE SHOWING VARIATION IN AMOUNT OF WHITE SPOTTING

Cross		Types Observed and Expected Classified According to Ranges Given in Table I					Mean Grade (M.) and Standard Deviation (S.D.) for the Larger Distributions							
							Black-eyed White		"Spotted"[6]		Type A		Piebald	
		Black-eyed White	"Spotted"[6]	Type A	Piebald	Self	M.	S.D.	M.	S.D.	M.	S.D.	M.	S.D.
1. Black-eyed white×piebald (*Wwss* × *wwss*)	Observed	160			163		83.8±.6	11.3±.4					12.5±.6	11.2±.4
	Expected	161.5			161.5									
2. Black-eyed white × self (*Wwss* × *wwSS*)	Observed			40		36					9.5±1.1	10.9±.9		
	Expected			38		38								
3. Type A × piebald (*WwSs* *wwss*)	Observed	113	214			116	84.7±.6	10.3±.5	11.6±.5	11.3±.4				
	Expected	110.7	221.5			110.7								
4. Type A × Type A (*WwSs* × *WwSs*)	Observed	16	27			18								
	Expected	10.2	35.5			15.2								
5. Type A × self (*WwSs* × *wwSS*)	Observed		27			33								
	Expected		30			30								
6. Type C × piebald (*WwSS* × *wwss*)	Observed			43		42					6.7±.5	5.06±.4		
	Expected			42.5		42.5								
7. Black-eyed white × black-eyed white (*Wwss*×*Wwss*)	Observed	13			4									
	Expected	11.3			5.7									
8. All black-eyed whites (*Wwss*)							83.5±.4	11.4±.3						
9. All Type "A" (*WwSs*)											7.9±.6	8.4±.4		
10. F_2 piebalds from cross of piebald × self (*wwss*)													8.0±.3	7.0±.2
11. All piebalds[9] (*wwss*)													9.7±.3	8.6±.2

than the darker piebalds. The difference in the means of white spotting in the offspring of the two crosses is significant when the errors are considered.[4] When we consider the kinds of individuals produced, we find that the darker piebalds produce certain classes of young which the lighter piebalds do not produce. The darker piebalds appear to possess then a factor or factors determining an increase in the amount of pigment produced and a consequent decrease in the amount of the white spotting. The lighter piebalds do not give evidence of possessing these genes or if they do possess certain of them they do not at any rate possess the number or the kinds which are apparent in the darker piebalds. It is to be especially noted that such modifying genes produce effects equally on the amount of black-eyed white spotting and on the amount of piebald spotting.

In the above case the assumed modifying genes came from piebalds differing in amounts of white spotting. In crosses 3 and 4 (Table III) their effect has been tested when entering in connection with black-eyed white spotting. The spotting produced in Type "A"s (*WwSs*) must be due to the gene *W* for animals of the formula *Ss* are not spotted except for certain imperfections of dominance already noted. Darker Type "A"s (0–10 per cent. white dorsally) and lighter Type "A"s (more than 10 per cent. white) were tested by mating with piebalds of various grades ranging from 20 per cent. white to 0 per cent white. The young from darker Type "A"s $\times$ piebald (Cross 3) were of three sorts as expected, black-eyed whites, "spotted" (comprising Type "A"s and piebalds) and selfs in the approximate ratio of 1:2:1. The mean of the black-eyed whites was $81.3 \pm .8$ per cent. white, which is about the same as the mean of black-eyed whites out of dark piebalds. They varied from 100 per cent. to 56 per cent. white with a standard deviation of $10.3 \pm .6$. The "spotted" young from this cross had a mean grade of 8.6 per cent. $\pm$ .5, a range

[4] The difference in mean grade of offspring of lighter and darker parents is 8.0 ± 1.06, or more than 7 times the probable error.

TABLE III

CROSSES OF BLACK-EYED WHITE AND TYPE "A" MICE OF VARIOUS GRADES WITH PIEBALD MICE TO ASCERTAIN GENETIC SIGNIFICANCE OF VARIATION IN AMOUNT OF WHITE SPOTTING

Distribution of Young with Various Amounts of Dorsal White

Cross	100–96	95–91	90–86	85–81	80–76	75–71	70–66	65–61	60–56	55–51	50–46	45–41	40–36	35–31	30–26	25–21	20–16	15–11	10–6	5–0	Self	Total	Black-eyed Whites			"Spotted"		
																							M.	S.D.	Total	M.	S.D.	Total
1. Black-eyed whites of all grades × piebalds less than 10% white dorsally	8	16	21	24	11	10	10	6	6	3	1	1	1	1	2	8	11	18	39	31		228	80.5±.7	11.6±.5	115	10.9± .4	8.1±.3	113
2. Black-eyed whites of all grades × piebalds more than 10% dorsally	5	18	13	3	1	2	3	0	0	0	1	0	4	2	3	5	6	6	7	11		90	88.5±.8	7.8±.5	45	16.4±1.2	12.1±.8	45
3. Type "A's" less then 10% white dorsally × piebalds of all grades	4	9	18	16	10	5	7	3	4	0	2	0	2	1	4	3	11	11	33	72	85	300	81.3±.8	10.3±.6	76	8.6± .5	8.9±.3	139
4. Type "A's" more than 10% white dorsally × piebalds of all grades	11	14	5	4	3	0	0	0	0	0	3	2	4	5	6	3	10	10	12	17	37	146	91.7±.7	6.19±.5	37	17.2±1.0	13.2±.7	72

from 50 to 0 per cent. white and a standard deviation of $8.9 \pm .3$.

In Cross 4 the piebald parents were of similar grades to those used in Cross 3 while the Type "A" parents were all *more* than 10 per cent. white dorsally. The black-eyed white young from this cross had a mean grade of $91.7 \pm .7$ per cent. white. They varied from 100 per cent. to 76 per cent. white with a standard deviation of $6.19 \pm .5$. The "spotted" young (Type "A" and piebald mixed) were of mean grade 17.2 ± 1.0 per cent. white, and varied from 50 per cent. to 0 per cent. white, with a standard deviation of $13.2 \pm .7$. In general the offspring of the lighter Type "A" parents were characterized by about 10 per cent. more white spotting than the offspring of the darker Type "A" parents. The difference of the parents in amount of spotting is thence reflected in similar differences in their respective offspring.

The indications from the tests of Type "A" spotted mice are that the same modifying factors which were assumed to cause the variation in the amount of spotting in piebalds cause also the variation in the expression of the gene *W* as evidenced in Type "A" spotting. Here also certain classes of dark black-eyed whites appear when dark Type "A"s are bred which are absent from the young produced by lighter Type "A"s. This absence is witnessed by the significantly lower variabilities of the black-eyed white offspring of both lighter piebald and lighter Type "A"s. The effect of the modifiers is the opposite when acting on the piebald and spotted offspring of these crosses. The piebald offspring of lighter piebald and Type "A" parents have a *greater* range and consequently a *higher* standard deviation than the piebald offspring of darker parents. The darkening modifiers *add* darker classes to the black-eyed white range but *subtract* from the lighter classes of piebald, lowering in general the amount of white in each type. A "light" piebald, namely, one near the upper limit of piebald spotting and lacking the dark modifiers, may thus be similar in appearance to a "dark" black-eyed white.

namely, one near the lower limit of black-eyed white spotting and possessing the dark modifiers. Such confusion is not apt to occur in the progeny of single pairs, for if the parents possess the modifiers dark black-eyed whites will be produced, but also dark piebalds, leaving an appreciable gap between the two types.

The Nature of the Modifiers

The effect of the same modifying genes upon the expression of both black-eyed white and piebald spotting furnishes certain information concerning the nature of the modifying genes themselves. The main spotting genes *W* and *s* have been found to be properties of distinct loci in different chromosomes (Dunn, 1920). Therefore the gene or genes which modify both *W* and *s* must determine the general conditions underlying the formation of pigment in the coat rather than specific conditions associated with a particular spotting gene. From the present evidence it appears to the writer that these modifying genes alter the internal environment of enzyme and chromogen upon which the main spotting genes *W* and *s* act to bring about their specific effects. The darkening modifiers appear to increase the general *amount* of color forming substance. In the presence of such modifiers both *W* and *s* produce relatively less than the normal amount of white spotting.

The Source of the Modifiers

The genes modifying the amount of white spotting in the mice used in these experiments appear to have come from certain self mice with which black-eyed whites and piebalds had been crossed. The black-eyed white stock used was originally bred by Dr. J. A. Detlefsen and reached this laboratory through a fancier. When first bred *inter se* no grading records were kept, but I am certain that no black-eyed whites were produced which were less than 70 per cent. white. This agrees fairly well with the range of the black-eyed whites bred by Little. The

piebalds used were obtained originally from fanciers. Sixty-five such piebalds varied from approximately 50 per cent. white to 0 per cent. white dorsally, with a mean grade of about 22 per cent. white dorsally. When these had been crossed with self mice 278 piebalds extracted in the second generation averaged 8 per cent. white dorsally. Their range was approximately the same as that of the original piebalds but the darker classes between 0–10 per cent. white had been greatly enlarged. It is probably from this cross that the darkening modifiers were introduced into the piebald stock, for the piebalds used in all subsequent crosses were descended from these extracted piebalds, most of which showed but little white spotting. It might be supposed that the darkness of the extracted piebalds could be explained on the basis of contamination of the piebald gene during its residence in self animals. That this is not the true explanation is indicated by other results. The cross of black-eyed white × piebald (Table II, Cross 1) yields black-eyed white progeny with a mean grade of 82.8 per cent. and piebalds averaging 12.5 per cent. The cross Type "A" × piebald (Table II, Cross 3) yields black-eyed white young with a mean grade of 84.8 per cent. white and "spotted" young, with a mean grade of 11.6 per cent. white. The means in the two crosses do not differ sensibly. Yet Type "A" is heterozygous for self and the young it produces should exhibit contamination if any takes place. Certain of the selfs with which piebalds were crossed originally, and certain selfs with which black-eyed whites were crossed later to produce Type "A"s appear to have contributed modifying genes which could have had no expression in the self mice, since these lacked the main spotting genes. Not all selfs are genotypically similar in respect to the modifiers, since from crosses of black-eyed whites with certain selfs has arisen a lighter strain of black-eyed white which is now being bred, while from other selfs has come a darker strain of black-eyed white which probably possesses the modifiers.

The probable existence of additional genes in mice of the nature of modifying factors has been stressed because it is felt that animals which can be easily bred in the laboratory should be thoroughly explored genetically, in order to find out characters not known at present. As the number of genes approaches the number of chromosomes, the probabilities of finding linkage become greater and it is through the investigation of linkage and the localization of the hereditary determiners that the most exact knowledge concerning the nature of the hereditary material can be secured.

Inheritance of Belly Spotting

Before concluding this discussion of modifiers of white spotting in mice some evidence may be added which bears on the appearance of a small amount of white spotting on the bellies of mice which are genetically self as regards *W* and *s*. Piebald spotting has been regarded as the recessive allelomorph of self or uniform coloration, and all the evidence from crosses between these two varieties supports this view. It has been noticed, however, that the heterozygotes resulting in F_1 are not always exact duplicates of the self parents. Where large numbers have been bred, investigators have always found F_1 animals with some white spotting, usually consisting of a patch of white on the belly not exceeding 12 per cent. of the ventral surface.

Records of experiments in the present investigation disclosed this apparent imperfection of dominance, and all animals resulting from the cross of piebald with self have been graded according to the per cent. of white spotting exhibited. A tabulation of these records shows that out of 51 pure piebalds bred to self mice, 36 produced only self mice with no white hairs; 15 produced some perfect self and some with white hairs. Of these 15 parents only 7 produced more than one young showing any white spotting. 557 young resulted from all piebald $\times$ self matings, of which 524 showed no trace of spotting

while 33, or about 6 per cent., showed one or more white hairs. The spotting in the F_1 mice was confined to the ventral surface,[5] usually in the center of the belly. The minimum size of this spot was a few white hairs, its maximum extent was 12 per cent. of the ventral surface, and its average extent was 3 per cent. of the ventral surface. All young produced by this cross must be regarded as selfs since all produced young, when interbred, in the ratio of three selfs to one piebald. What, then, is the cause of the appearance of certain animals in F_1 which show some characteristics of the recessive parent?

There may be two answers to this question: (1) the apparent imperfections of dominance in F_1 may be due to fluctuations in the somatic expression of the piebald gene when present singly in the zygote; (2) they may be due to a definite gene or genes for a small amount of ventral spotting in mice heterozygous for piebald.

As evidence for the first view we have relevant data in the experiments just reported. An analysis reveals that the production of young with small amounts of white spotting is not correlated with the somatic appearance of the piebald parents since in amount and distribution of spotting these parents as a class are not distinguishable from the parents which produced only true self young. On the other hand, practically all the spotted F_1s which were produced by individual piebald parents had for their other parent a particular self animal. Apparently the selfs as well as the piebalds varied in the power of producing slightly spotted young. Causes influencing the production of this small amount of spotting in F_1 may have been contributed by the self parents, although the posibility that part of the causes came from the piebald parents is not excluded by the evidence. If this be accepted as evidence that selfs share in the production of slightly spotted mice, then certain selfs must differ genetically from other selfs, and the point of difference may be a separate recessive factor for ventral

[5] With the exception of the few dorsally spotted mice referred to on p. —.

spotting, which is expressed in the presence of but one dose of piebald.

On this view, self animals which, when bred to piebalds, produce animals with small amounts of ventral spotting, must be heterozygous for a recessive gene for such spotting. Moreover, the piebald parents must also be heterozygous in the same gene. This is required by the evidence. 15 pairs of parents producing young with some white gave a total of 151 young, of which 33, or 21 per cent., showed some white. This is nearly a ratio of three perfect selfs to one with some white, and if the cause of the small spotting is a gene, both piebald and self parents must have been heterozygous for it. The presence of such a gene in piebald mice is difficult of demonstration, since when bred together piebald mice produce only piebalds, with their characteristic dorsal and ventral spotting, which obscures the action of any genes for spotting of the ventrum only.

A summary now partially completed shows that the peculiarity of small belly spotting in "self" mice does not breed true. Matings of "belly spot" × "belly spot" have produced 70 young of which 57 were graded as self (viz., having either no white spotting or less than 12 per cent. white ventrally) while 13 were clearly piebald. Individual tests showed that all belly spotted mice bred were heterozygous for piebald, so this ratio is probably a deviation from a 3:1 ratio. Of the 57 "selfs," 41 had some ventral spotting like the parents, while 16 were true selfs without any white hairs. The appearance of these true selfs, and the fact that all belly spotted mice tested were heterozygous for piebald indicate that the assumed gene for belly spotting is only expressed by mice which are heterozygous for piebald. The total distribution from the matings just referred to resembles somewhat a 1:2:1 ratio, which would be expected if selfs heterozygous for piebald show by reason of an imperfection in dominance, a small amount of ventral spotting. The distribution tabulated on this assumption follows:

	Self (*SS*)	Self (Belly-Spot) *Ss*+×	Piebald *ss*	Total
Observed	16	41	13	70
Expected	17.5	35	17.5	70

That the variation is inherited is argued by the much greater frequency of belly spotted individuals in the offspring of parents showing the characteristic than in the total progeny of all self × piebald matings. In the progeny of belly spotted mice 71 per cent. of all selfs were belly spotted, while of all selfs heterozygous for piebald only 6 per cent. were belly spotted. The problem is doubtless complicated (as are probably all spotting problems) by the occurrence of a certain amount of uncontrollable somatic variation in the expression of the genes, by reason of which the truly genetic variations cannot always be isolated with certainty. In addition the last mentioned modifier seems to be dependent for expression on a particular complex of genes, namely, the presence in one individual of one dose of piebald and one of its normal allelomorph (*Ss*).

SUMMARY OF MODIFIERS OF AMOUNT OF WHITE SPOTTING

1. The expresson of the complex of genes producing black-eyed white spotting (*Wwss*) is subject to modification by a gene or genes determining an increased amount of pigment and a decreased amount of white spotting. The normal range of black-eyed whites being from 100 to 70 per cent. white dorsally, the addition of such darkening modifiers decreases the mean amount of white spotting in such a fashion that the range is extended to as low as 50 per cent. white.

2. The expression of the gene for piebald spotting is subject to modification in the same direction and by the same gene or genes which modify the expression of black-eyed white. When these darkening modifiers are present in mice pure for piebald (*ss*) most of the mice are

about 10 per cent. or less white dorsally, while those with larger percentage of white are much rarer than among piebalds lacking the darkening modifiers.

3. The genotype *Ss* ordinarily produces the self coat, but in the presence of an additional modifying gene produces a small amount of white spotting on the ventral surface, varying in size from a few white hairs to 12 per cent. of that surface.

Modifiers Affecting Localization of White Spotting in Piebald Mice

The presence of separate genes for certain localizations of spotting in piebald mice has been suspected for some time. Fanciers, for instance, have given separate names to such types as "Dutch belted" mice and have claimed that they bred true to this condition, which resembles the Dutch belted pattern of cattle. Consequently when piebald mice showing distinct localization of white spotting in the pelt have been born in these experiments they have been saved for further study.

The most striking of these localized spotting types has appeared sporadically in the piebald stock. From its appearance I have called it "white face" although it varies from a small blaze of white on the forehead to a white spot which covers the whole head back as far as the ears. The belly is spotted with white as in ordinary piebalds. The strain of white face which has been isolated breeds true to this condition, 8 matings of white-face by white face having produced 46 young, all of them white faced. The offspring of one pair of white faced mice which were brother and sister, have been inbred, brother to sister, for four generations and there have been born in these matings to date 36 young, all white faced, and varying but little in the amount and distribution of the white spotting on the face.

One other sub-type of piebald is perhaps also separable. This is the type known as belted. It varies

from a wide white belt covering all of the back from shoulders to hind limbs (about 45 or 50 per cent. of the dorsal surface) down to a small spot located likewise on the back within this same area. The rest of the dorsum including the face is colored. The belly is spotted with white as in ordinary piebalds. Several good examples of this type have been saved and a few matings have been made recently. Only two matings of belted by belted have produced young. All of these young (four in number) are belted, with no spotting elsewhere on the dorsum. This is hardly a sufficient test of the separateness of this type, but more data are being accumulated.

It seems fairly evident that the production of the pattern of piebald mice is due to a complex of genes modifying the expression of one main gene. It is probable that each such gene in the complex determines the nondevelopment of pigment in one part of the pelage. As a means of testing these hypotheses and of separating, if present, the various causative factors, the inbreeding method advanced by East warrants a trial as the most likely to bring results. Piebald mice of several different types should be inbred and the inbreeding continued in the various lines, brother to sister, for seven or eight generations. This should result in the purification of the types by the elimination of heterozygotes, and the resulting pure recessives should exhibit, if present, the effects of the separate factors. Such inbreeding is now under way on the white face and on the belted types.

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STRUCTURAL CHARACTERISTICS OF THE HAIR OF MAMMALS

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THE microscopic structures in the hairs of mammals offer certain definite and unchanging characteristics which have been found useful for the purposes of identification.[1] The present paper aims to be an answer to numerous inquiries which the writer has received regarding: (1) the structure of a large number of mammal hairs, with especial reference to the possibility of systematically classifying them upon some morphologically accurate basis; (22) the relationships between the various elemental structures of the hair shaft; and (3) the methods employed in the preparation of the hairs for microscopic analysis.

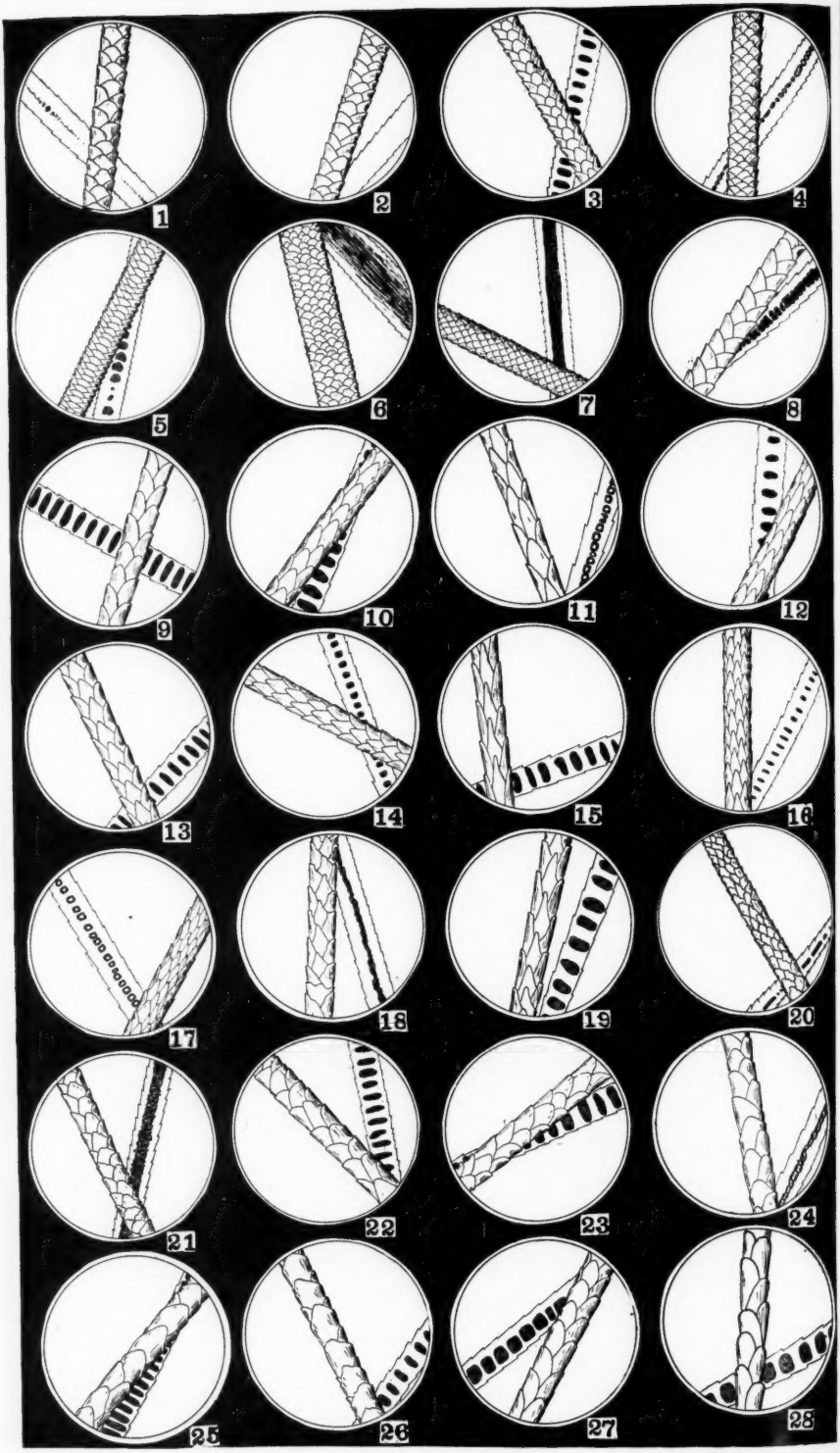
The primary development of the hair begins as a localized proliferation of the cells of the outermost layer of the skin, known as the epidermis, forming a dense aggregation of cells which elongates downward into the corium, or dermis, beneath. Directly underneath this downward-elongated, flask-shaped depression of the cells of the epidermis there is formed a dense mass composed of cells of the corium, or dermis, which ultimately becomes the papilla of the hair (*P*, Fig. 178). The flask-shaped depression now becomes lined with cells of the epidermis, and is called the follicle. The epithelial contents of the growing follicle elongate into an avial strand of fusiform, spindle cells, which later undergoes keratinization, or becomes horny, and forms the hair shaft. The lower portion of the shaft expands into a bulb which en-

[1] Hausman: (1) "The Microscopic Identification of Commercial Fur Hairs," *Scientific Monthly*, Jan., 1920, pp. 70–78; (2) "A Micrological Investigation of the Hair Structure of the Monotremata," *Am. Journal of Anatomy*, Sept., 1920, (3) "The Microscopic Identification of Mammal Hairs Used in the Textile Industry," *The Scientific American*, Feb. 21, 1920.

wraps the papilla (Fig. 178). The shaft elongates upward, and emerges through the epidermis, an aperture thereafter known as the mouth of the follicle, and continues to grow, the growth being exclusively confined to the bulbous lower, or proximal portion of the shaft. Here the conversion of matrix cells into keratinized hair shaft cells continually progresses. Mammal hairs are in general either circular or elliptical in cross section.[2] Those which are circular are straight, or but slightly curved, while those of elliptical cross section are curly or kinky, the amount of curl being dependent upon the flatness of the ellipse.

The hair shaft consists of four structural units (Figs. 167 and 168): (1) the *medulla,* sometimes termed the pith, from a somewhat analogous structure in plant stems, and which is built up of many shrunken and variously disposed cells or chambers, representing dried and cornified epithelial structures connected by a branching filamentous network, which sometimes completely fills the medullary column, but which is interrupted in many cases; (2) the *cortex,* or shell of the hair shaft, surrounding the medulla, and composed of elongate, fusiform cells or hair-spindles, coalesced together into a horny, almost homogeneous, hyaline mass and forming in many cases, where the medulla is reduced, a large proportion of the hair shaft; (3) the *pigment granules,* to which the color of the hair is primarily due (though in some hairs the pigment is diffuse and not in granular form), scattered about within or between the hair spindles, and in some hairs arranged in definite patterns; and (4) the *cuticle,* or outermost integument of the hair shaft, lying upon the cortex, and composed of imbricated, thin, hyaline, colorless scales of varying forms and dimensions. It is the forms, relationships, and measurements of these four elements, together with the measurements of the diam-

[2] The pioneer work in the relation of the shape of the cross section of human hair in its waviness to Dr. Pruner-Bey's "De La Chevelure comme Characteristique des Races Humaines, d'après des Recherches Microscopiques," in *Mémoires de la Société d'Anthropologie de Paris,* Vol. 2, p. 1.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eter of the hair shaft itself, in micra[3] which constitute the series of determinative criteria for each species of hair.

Medullas can be conveniently grouped, according to their forms, as they: (1) *discontinuous,* as in the hair of the Botta's pocket gopher (*Thomomomys bottæ*) (Fig. 3); (2) *continuous,* as in the hair of the kinkajou (*Cercoleptes caudivolvulus*) (Fig. 7); and (3) *fragmental,* as in the hair of the wombat (*Phascolomys ursinus*) (Fig. 64).

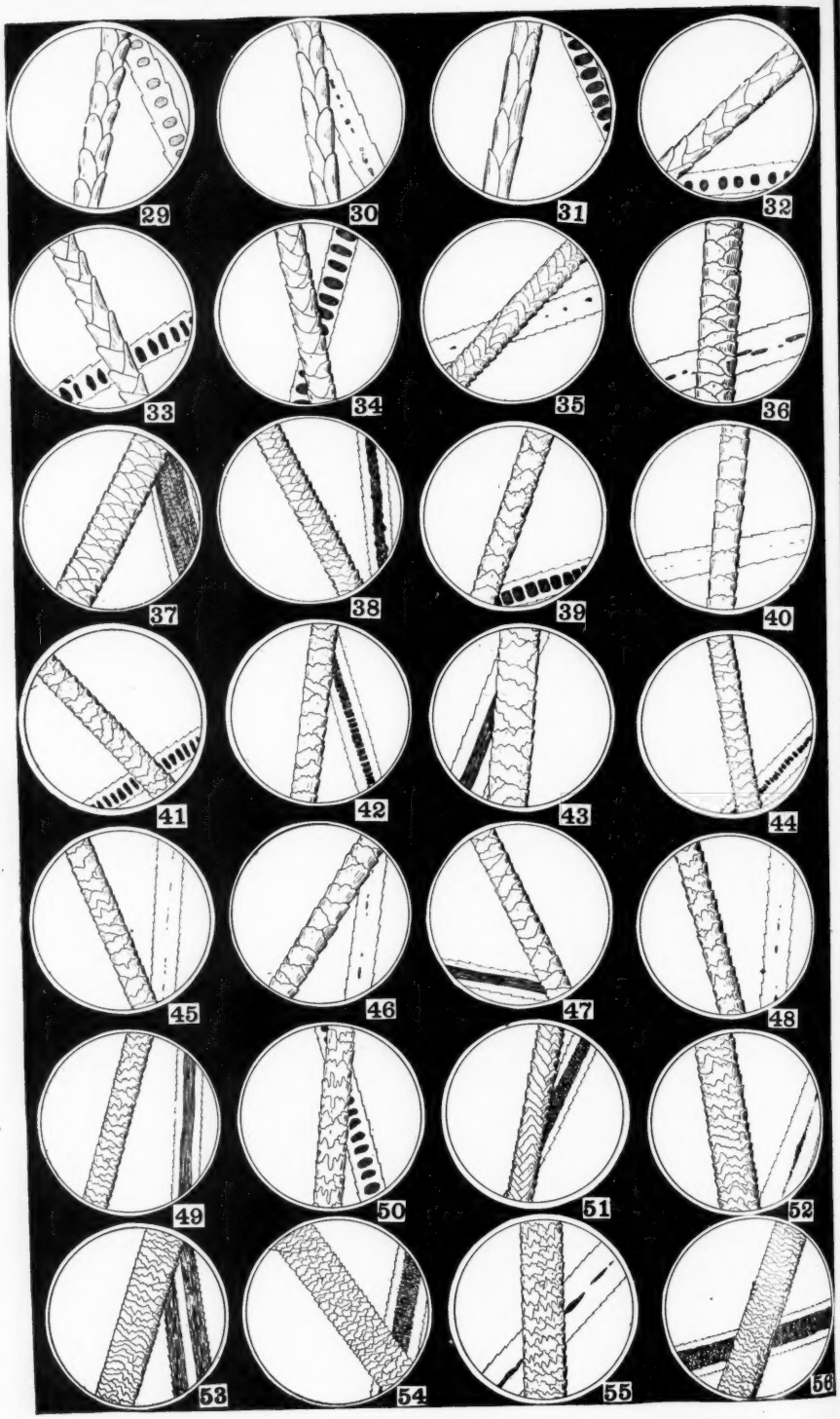
The cuticular scales fall readily into two well-marked types, the: (1) *imbricate,* represented in the hair of the civet (*Arctogalidia fusca*) (Fig. 1); and (2) *coronal,* represented in the hair of the majority of the bats, *e.g.,* the mastiff bat (*Molossus sinaloæ*) (Fig. 105).

The cortex element of the hair shaft structure exhibits few or no traces of the form of its component fusiform

EXPLANATION OF PLATE I

FIG. 1. Civet (*Arctogalidia fusca*), 21.00 μ.
FIG. 2. Pocket Kangaroo Rat (*Dipodomys m. nitratus*), 12.00 μ.
FIG. 3. Botta's Pocket Gopher (*Thomomys bottæ*), 25.50 μ.
FIG. 4. Coypu Rat (*Myocastor coypus*), 11.00 μ.
FIG. 5. Black Lemur (*Lemur makaka*), 20.00 μ.
FIG. 6. Chimpanzee (*Anthropopithecus troglodytes*), 119.00 μ.
FIG. 7. Kinkajou (*Cercoleptes caudivolvulus*), 34.00 μ.
FIG. 8. Rocky Mt. Jumping Mouse (*Zapus princeps*), 20.00 μ.
FIG. 9. Sierra Jumping Mouse (*Zapus trinotatus alleni*), 17.00 μ.
FIG. 10. Orolestes (*Orolestes obscurus*), 10.00 μ.
FIG. 11. Cacamixtli (*Bassariscus astutus flavus*), 17.00 μ.
FIG. 12. Striped Bandicoot (*Perameles bougainvillei bougainvillei*), 17.00 μ
FIG. 13. European Mole (*Talpa europæa*), 17.00 μ.
FIG. 14. Platypus (*Ornithorhynchus anatinus*), 8.00 μ.
FIG. 15. Star Nosed Mole (*Condylura cristata*), 25.50 μ.
FIG. 16. Pigmy Flying Phalanger (*Acrobates pygmæa*), 17.00 μ.
FIG. 17. Black Bear (*Ursinus americanus*), 27.00 μ.
FIG. 18. Red Kangaroo (*Macropus rufus*), 25.50 μ.
FIG. 19. Microgale (*Microgale dobsoni*), 18.80 μ.
FIG. 20. Aye aye (*Chiromys madagascariensis*), 24.00 μ.
FIG. 21. Koala (*Phascolarctos cinereus*), 20.40 μ.
FIG. 22. Dormouse (*Muscardinus pulcher*), 17.00 μ.
FIG. 23. House Mouse (*Mus musculus*), 17.00 μ.
FIG. 24. Gymnura (*Gymnura gymnura gymnura*), 19.00 μ.
FIG. 25. Woodland Jumping Mouse (*Napeozapus insignis insignis*), 21.00 μ
FIG. 26. Loir (*Glis glis glis*), 30.00 μ.
FIG. 27. Rat (*albino*) (*Mus norvegicus*), 17.50 μ.
FIG. 28. Hoy's Shrew (*Microsorex hoyi*), 18.00 μ.

[3] One micron (μ) is 1/1,000 of a millimeter, or circa 1/254,000 of an inch.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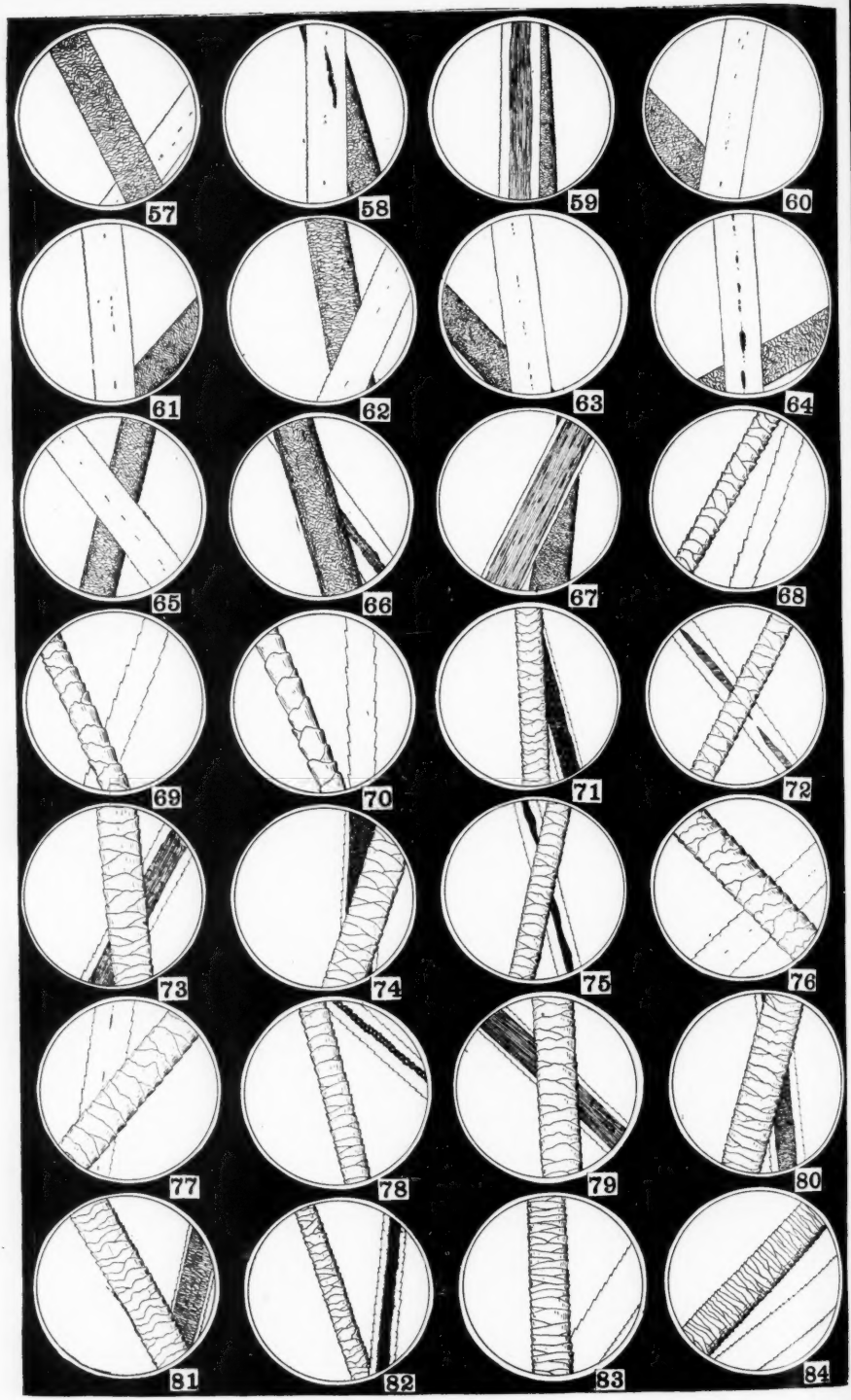
cells, or hair spindles, except under dissociative treatment with caustic soda, caustic potash, or acids of various sorts, and hence is of very little value as a criterion for determining the species of the hair.

The coloring matter, or pigment, of the hair shaft is either distributed diffusely and homogeneously throughout the cortex, or exists as an aggregation of granules between or within the fusiform cortical cells, or hair tween or within the fusiform cortical cells, or hair spindles. Where the latter is the case the granules appear to be of definite form and mode of placentation for each species of hair. In many cases, it is believed that the characteristic patterns formed by the arrangement of the pigment granules, as well as the form of the granules themselves may offer a valuable character for identification. Figs. 190, 191, and 192 show respectively portions of the hair shafts of the mandril (*Cyanocephalus maimon*), badger (*Taxidea americana*), and wolverene (*Gulo luscus*), very highly magnified, illustrative of the differences which may exist in the configuration and ar-

EXPLANATION OF PLATE II

FIG. 29. Geogale (*Geogale aurita*), 12.00 μ.
FIG. 30. Potamogale (*Potamogale velox*), 10.10 μ.
FIG. 31. Golden Mole (*Amblysomus corriæ*), 13.00 μ.
FIG. 32. Heliophobius (*Heliophobius kapiti*), 15.00 μ.
FIG. 33. Marsh Shrew (*Neosorex palustris navigator*), 11.30 μ.
FIG. 34. Rock Runner (*Petrodromus tetradactylus*), 37.00 μ.
FIG. 35. Speke's Jumping Mouse (*Pectinator spekii*), 25.00 μ.
FIG. 36. Walrus (*Trichechus rosmarus*).
FIG. 37. American Wapiti (*Cervus canadensis*), 94.00 μ.
FIG. 38. Mongoose Lemur (*Lemur mongoz*), 20.00 μ.
FIG. 39. Colugo (*Galeopithecus volans*), 20.50 μ.
FIG. 40. Coendou (*Coendou sanctæmartæ*), 25.00 μ.
FIG. 41. Flying Squirrel (*Sciuropterus volucella*), 11.70 μ.
FIG. 42. Bactrian Camel (*Camelus bactrianus*), 34.00 μ.
FIG. 43. Tiger (*Felis tigris*), 68.00 μ.
FIG. 44. Bruce's Dassie (*Procavia brucci rudolphi*), 22.00 μ.
FIG. 45. Dassie (*Procavia capensis*), 25.50 μ.
FIG. 46. Coendou (*Coendou mexicanus*), 38.00 μ.
FIG. 47. Proboscis Monkey (*Nasalis larvatus*), 47.60 μ.
FIG. 48. Spider Monkey (*Ateles geoffroi*), 32.00 μ.
FIG. 49. Great Gray Kangaroo (*Macropus giganteus*), 25.50 μ.
FIG. 50. Common Dasyure (*Dasyurus viverrinus*), 17.00 μ.
FIG. 51. Capybara (*Hydrochærus capybara*), 34.00 μ.
FIG. 52. Small Three-Spined Tenrec (*Hemicentetes variegatus*), 28.00 μ.
FIG. 53. Unau (*Cholœpus capitalis*), 68.00 μ.
FIG. 54. European Porcupine (*Hystrix cristata*), 140.00 μ.
FIG. 55. Spiny Anteater (*Tachyglossus hystrix*), 103.00 μ.
FIG. 56. Agouti (*Dasyprocta urucuna*), 150.00 μ.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rangement of the pigment granules. There seems to be also a wide variation in color value and color depth of the pigment granules, a variation which is especially well brought out by the use of reflected light, or of dark field illumination. These methods of examination will be explained later.

In a recent contribution to the structure of the mammalian hair[4] the author has pointed out that mammal hairs may be conveniently classified, on the basis of the configuration of the cuticular scales and medulla, as follows:

CUTICULAR SCALES

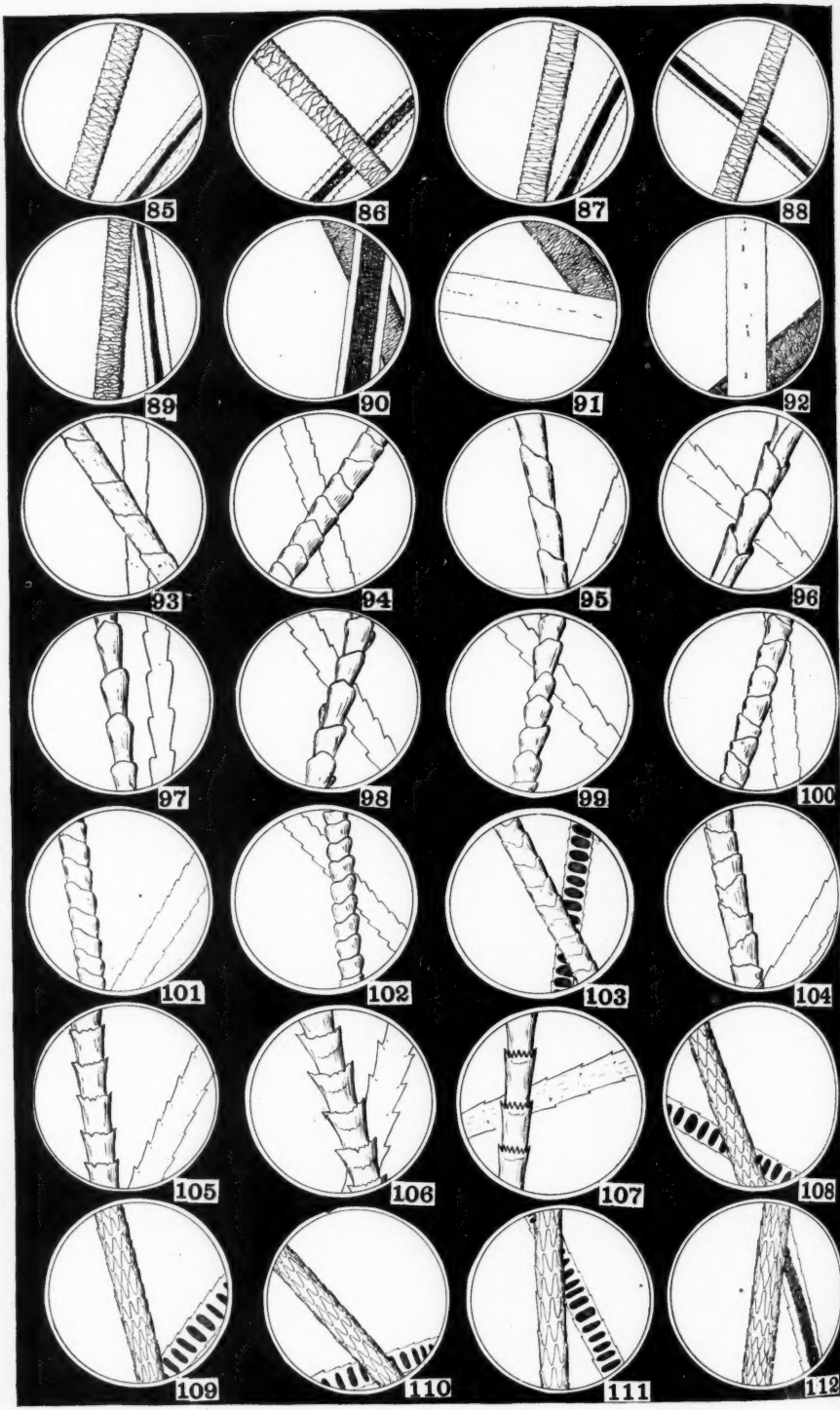
I. *Imbricate*

1. Ovate, represented by Figs. 1 to 7
2. Acuminate, represented by Figs. 8 to 20
3. Elongate, represented by Figs. 21 to 35
4. Crenate, represented by Figs. 36 to 67
5. Flattened, represented by Figs. 68 to 92

EXPLANATION OF PLATE III

FIG. 57. African Elephant (*Loxodonta africana capensis*), 80.00 μ.
FIG. 58. Ethiopian Aard Vark (*Orycteropus æthiopicus*), 252.00 μ.
FIG. 59. Hyena (*Hyæna hyæna schillingsi*), 122.00 μ.
FIG. 60. Richard's Seal (*Phoca richardi*), 232.00 μ.
FIG. 61. Two-Horned Rhinoceros (*Diceros bicornis bicornis*), 147.00 μ.
FIG. 62. Brush-Tailed Porcupine (*Ætherura africana*), 50.00 μ.
FIG. 63. Long-Tailed Pangolin (*Manis macrura*), 181.00 μ.
FIG. 64. Wombat (*Phascolomys ursinus*), 76.50 μ.
FIG. 65. Cape Aard Vark (*Orycteropus capensis*), 216.00 μ.
FIG. 66. Dinomys (*Dinomys brannicki*), 120.00 μ.
FIG. 67. Wild Boar (*Sus scrofa*), 680.00 μ.
FIG. 68. Two-Toed Anteater (*Cyclothurus didactylus*), 17.00 μ.
FIG. 69. Black-Faced Bat (*Melanycteris melanops*), 10.00 μ.
FIG. 70. Small Long-Tongued Fruit Bat (*Macroglossus minimus*), 13.00 μ.
FIG. 71. Chevrotain (*Tragulus boreanus*), 51.00 μ.
FIG. 72. Llama (*Lama glama*), 32.00 μ.
FIG. 73. Fox Terrier, 98.60 μ.
FIG. 74. Ingraham's Hutia (*Capromys ingrahami*), 76.50 μ.
FIG. 75. Jersey Cow, 42.50 μ.
FIG. 76. American Bison (*Bison americanus*), 77.00 μ.
FIG. 77. Manatee (*Manatus latirostris*), 136.00 μ.
FIG. 78. Pinche (*Midas oedipus*), 40.00 μ.
FIG. 79. Boschbok (*Tragelephus sylvaticus*), 119.00 μ.
FIG. 80. Sumatran Chevrotain (*Tragulus napu*), 55.70 μ.
FIG. 81. Hispid Pocket Mouse (*Perognathus hispidus*), 127.00 μ.
FIG. 82. Squirrel Monkey (*Chrysothrix sciurea*).
FIG. 83. Agouti (*Dasyprocta variegata*), 127.50 μ.
FIG. 84. Tamandua (*Tamandua tetradoctyla etensis*), 85.00 μ.

[4] Hausman: "A Micrological Investigation of the Hair Structure of the Monotremata," *Am. Journal of Anatomy*, Sept., 1920.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II. *Coronal*

1. Simple, represented by Figs. 93 to 102
2. Serrate, represented by Figs. 103 to 107
3. Dentate, represented by Figs. 108 to 113

Medullas

I. *Discontinuous*

A. Simple

1. Ovate, represented by Figs. 114 to 126
2. Elongate, represented by Figs. 127 to 128
3. Flattened, represented by Figs. 129 to 135

B. Compound

1. Ovate, represented by Fig. 136
2. Flattened, represented by Fig. 137

II. *Continuous*

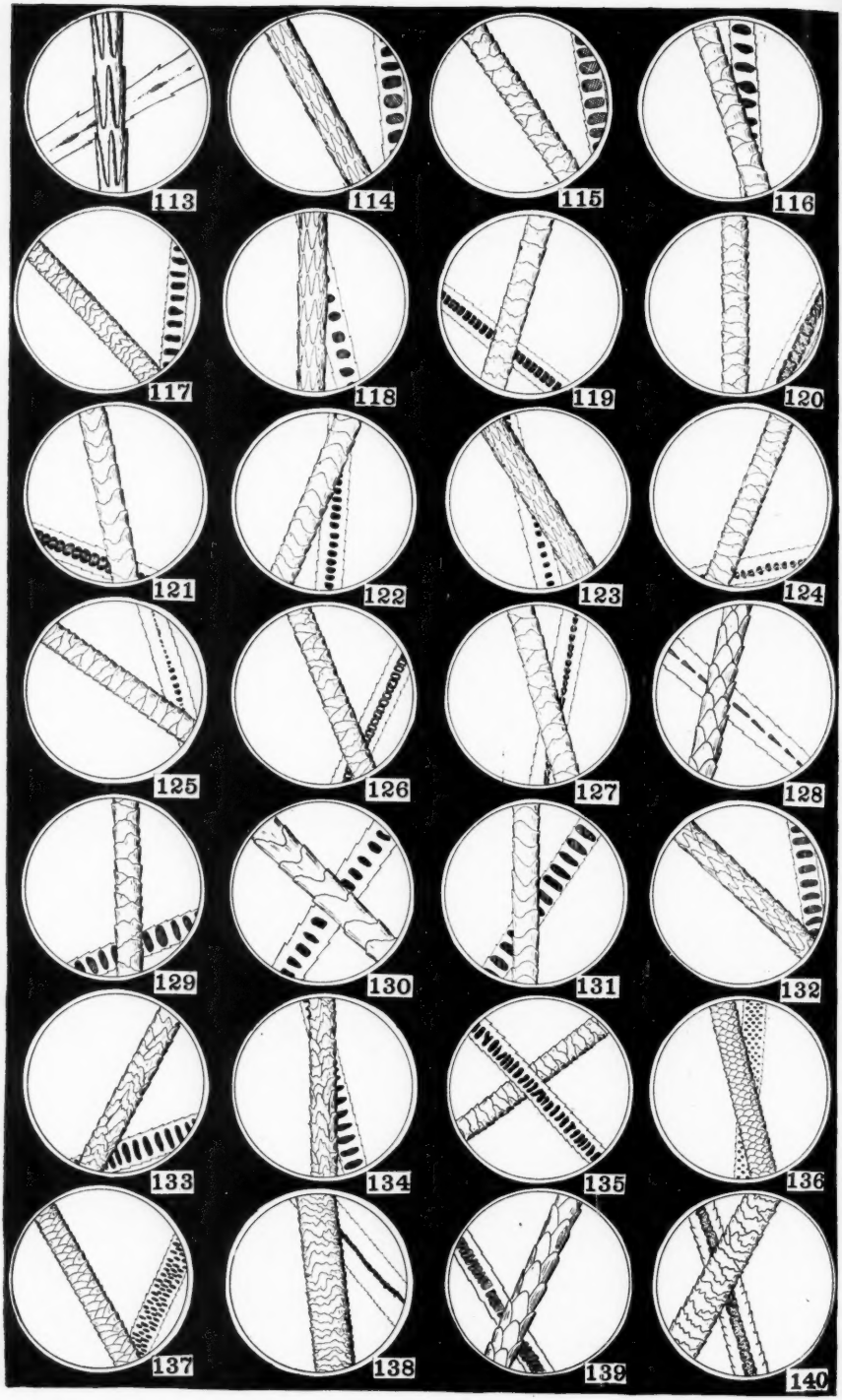
1. Nodose, represented by Figs. 138 to 147
2. Homogeneous, represented by Figs. 148 to 153

III. *Fragmental*

Represented by Figs. 115 to 166

EXPLANATION OF PLATE IV

Fig. 85. Gorilla (*Gorilla gorilla*), 37.40 μ.
Fig. 86. Virginia Deer (*Odocoilcus americanus*).
Fig. 87. Sifaka (*Propithecus coronatus*), 30.00 μ.
Fig. 88. Woolly Monkey (*Lagothrix infumatus*), 30.00 μ.
Fig. 89. Orang (*Simia satyrus*), 144.50 μ.
Fig. 90. Agouti (*Dasyprocta fuliginosa*), 190.00 μ
Fig. 91. Barbirussa (*Barbirussa alfurus*), 93.00 μ.
Fig. 92. Peccary (*Dicotyles tajuca*), 407.00 μ.
Fig. 93. Yapock (*Chironectes panamensis*), 11.30 μ.
Fig. 94. Natalus (*Natalus mexicanus*), 11.00 μ.
Fig. 95. Porto-Rican Bat (*Chilonycteris parnelli portoricensis*), 8.50 μ.
Fig. 96. Hammer-Headed Bat (*Eupomorphorus anurus*), 11.00 μ.
Fig. 97. Bicolored Leaf-Nosed Bat (*Hipposiderus fulvus*), 8.50 μ.
Fig. 98. Indian Vampire Bat (*Lavia frons*), 12.00 μ.
Fig. 99. Leaf-Nosed Bat(*Rhinolophus hainanus*), 10.00 μ.
Fig. 100. Horseshoe Bat (*Rhinolophus acuminatus*), 10.00 μ.
Fig. 101. Pipistrelle (*Pipistrellus subflavus*), 6.80 μ.
Fig. 102. Java Vampire Bat (*Petalia capensis*), 10.00 μ.
Fig. 103. Cape Mole Rat (*Tachyoryctes rex*), 17.00 μ.
Fig. 104. Phyllops (*Phyllops falcatus*), 10.00 μ.
Fig. 105. Mastiff Bat (*Molossus sinaloae*), 9.00 μ.
Fig. 106. Wrinkled-Lipped Bat (*Nyctinomus bocagei*), 8.50 μ.
Fig. 107. Intermediate Bat (*Mormops intermedia*), 6.80 μ.
Fig. 108. Chief Pika (*Ochotona princeps*), 13.60 μ.
Fig. 109. Pika (*Ochotona figginsi*), 11.30 μ.
Fig. 110. Pika (*Ochotona wardi*), 11.30 μ.
Fig. 111. Alpine Chinchilla (*Lagidium pernarum*), 11.30 μ.
Fig. 112. Little Banded Anteater (*Myrmecobius fasciatus*), 20.40 μ.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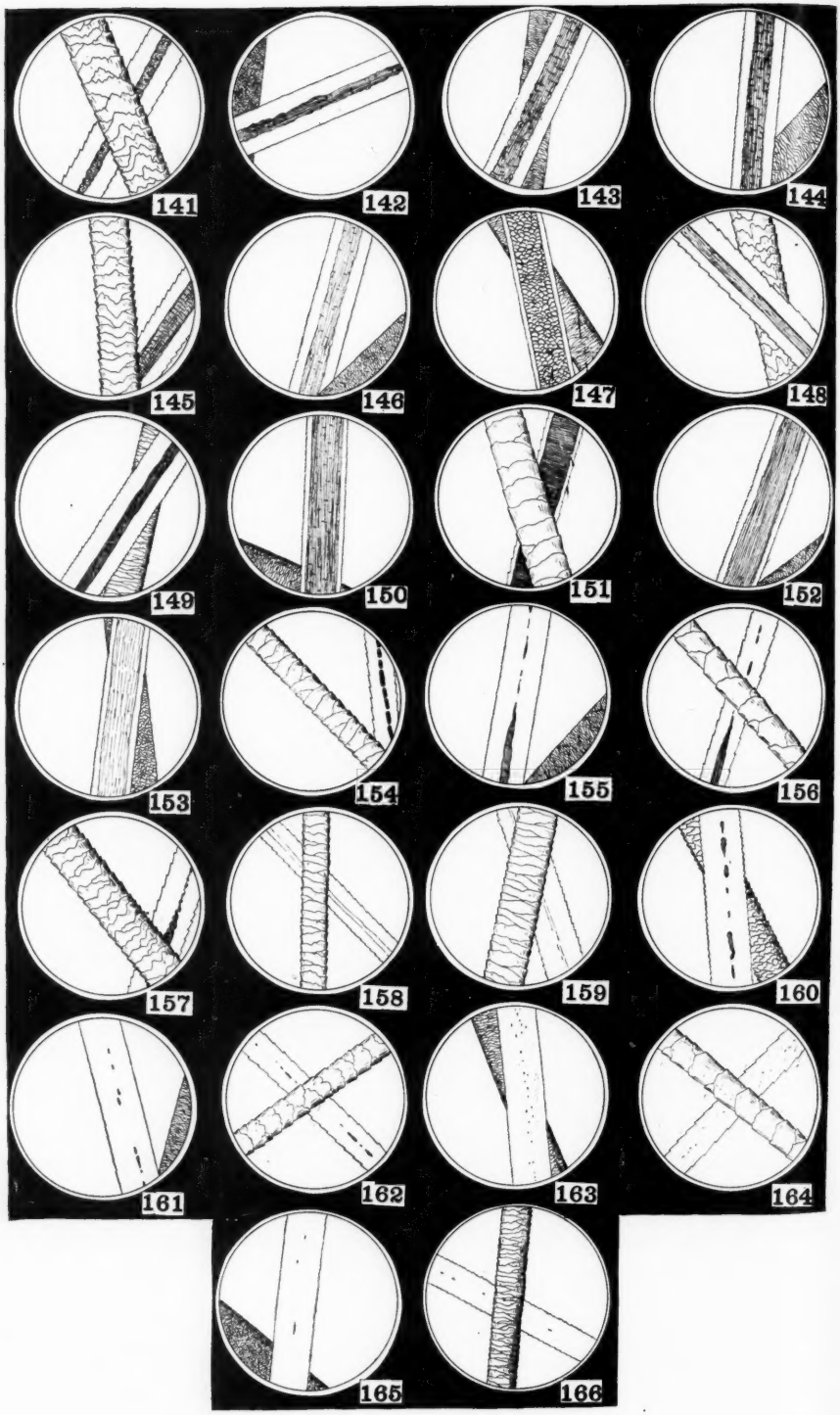
The hair type chosen to be shown as the most representative of each species is that type which, it was found, in most cases constitutes the major portion of the body covering, *i.e.*, the *fur*, or *under hair*. This usually underlies a comparatively more or less sparse growth of longer, coarser, stouter hair, which is termed the *protective*, or *over hair*. In typically aquatic mammals, such as the seals, walruses, etc., the protective hair is thicker than in those forms which are merely amphibious, such as the platypus, muskrats, beavers, etc. In such mammals as the whales, porpoises, etc., which are wholly aquatic, the fur hair has apparently vanished altogether. The only remaining hairs upon the body are, as a rule, confined to a very few stout stubs of hairs, located commonly in the region about the muzzle. In such hairs the cuticular scales are always of one type, illustrated by the muzzle hair of the dugong (*Dugong dugong*) (Fig. 159).

In identification, however, it is sometimes necessary to prepare for examination shafts of both the fur and the

EXPLANATION OF PLATE V

FIG. 113. European Otter (*Lutra vulgaris*), 10.00 μ.
FIG. 114. Chinchilla (*Chinchilla lanigera*), 16.00 μ.
FIG. 115. Dusky-Handed Tarsier (*Tarsius fuscus*), 13.00 μ.
FIG. 116. Elephant Shrew (*Macroscelides proboscideus*), 20.00 μ.
FIG. 117. Red Squirrel (*Sciurus hudsonicus*), 17.00 μ.
FIG. 118. Sewellel (*Aplodontia rufa*), 17.00 μ.
FIG. 119. Marsupial Mole (*Notoryctes typhlops*), 17.00 μ.
FIG. 120. Galeopterus (*Galeopterus gracilis*), 22.00 μ.
FIG. 121. Beecroft's Scale-Tailed Squirrel (*Anomalurus beecrofti*), 18.00 μ
FIG. 122. Viscacha (*Lagostomus maximus*), 41.00 μ.
FIG. 123. Black-Footed Ferret (*Putorius nigripes*), 20.40 μ.
FIG. 124. Nail-Tailed Wallaby (*Onychogale unguifera*), 18.50 μ.
FIG. 125. Foussa (*Cryptoprocta ferox*), 22.00 μ.
FIG. 126. Cavy (*Dolichotis salinicola*), 34.00 μ.
FIG. 127. Peters' Shrew (*Rhyncocyon petersi*), 26.00 μ.
FIG. 128. Racoon (*Procyon lotor*), 20.00 μ
FIG. 129. Philippine Tarsier (*Tarsius philippinensis*), 18.00 μ.
FIG. 130. Great Mole Rat (*Spalax typhlus*), 17.00 μ.
FIG. 131. Idiurus (*Idiurus zenkeri*), 9.10 μ.
FIG. 132. Nelson's Hare (*Romerolagus diazi*), 18.00 μ.
FIG. 133. Gray Rabbit (*Lepus nutalli mallurus*), 17.00 μ.
FIG. 134. Southern Varying Hare (*Lepus americanus virginianus*), 17.00 μ
FIG. 135. Black-Eared Marmoset (*Hapale jacchus*), 25.50 μ.
FIG. 136. Sennett Kangaroo Rat (*Perodipus sennetti*), 40.80 μ.
FIG. 137. Degu (*Octodon degus*), 34.00 μ.
FIG. 138. Agouta (*Solenodon paradoxus*), 83.00 μ.
FIG. 139. Canada Lynx (*Lynx canadensis*), 19.00 μ.
FIG. 140. European Hedgehog (*Erinaceus europeus*), 85.00 μ.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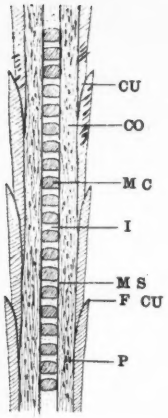
protective hair. And since the structural elements in these two types of hair usually differ considerably, a greater number of distinctive characters is thus available for comparison. However, the greater thickness and deeper pigmentation of the protective hair shafts make them much more difficult to work with than the finer, clearer fur hairs. Moreover, the scales of the protective hair are often worn off to such an extent as to make them also valueless as identification criteria. Figs. 175 to 177, and 169 to 171 show, represented to scale, the structure of the scales and medulla of the fur and protective hair of the skunk (*Mephitis mephitica*), and the European beaver (*Castor fiber*). The protective hair of mammals in general, in most cases, bears cuticular scales of the flattened or crenate type, and medullas of the continuous nodose or continuous homogeneous type.

In identifying hair species it is necessary to compare the scales and medulla from the same parts of the hairs[5]

EXPLANATION OF PLATE VI

FIG. 141. Polar Bear (*Thalarctos maritimus*), 68.00 μ.
FIG. 142. Hyena (*Hyæna hyæna bergeri*), 157.00 μ.
FIG. 143. Old World Tapir (*Tapirus terrestris*), 104.00 μ.
FIG. 144. American Tapir (*Tapirus americanus*), 74.00 μ.
FIG. 145. Langu (*Colobus caudatus matschei*), 88.00 μ.
FIG. 146. Central American Tapir (*Elasmognathus bairdi*), 96.00 μ.
FIG. 147. Rush Mouse (*Thryonomys gregorianus*), 165.00 μ.
FIG. 148. Hoffman's Sloth (*Cholœpus hoffmanni*), 68.00 μ.
FIG. 149. Ass (*Equus asinus*), 70.00 μ.
FIG. 150. Water Deer (*Hyomoschus aquaticum*), 122.00 μ.
FIG. 151. Thompson's Gazelle (*Gazella thompsoni nasalis*), 105.40 μ.
FIG. 152. Cape Giraffe (*Giraffa capensis*).
FIG. 153. Quagga (*Equus quagga bohmi*), 166.00 μ.
FIG. 154. Mongoose (*Helogale hirtula ahlselli*), 24.00 μ.
FIG. 155. Wart Hog (*Phacochœrus æthiopicus*), 357. 00 μ.
FIG. 156. Aard Wolf (*Proteles cristata*), 22.00 μ.
FIG. 157. Almiqui (*Solenodon cubanus*), 80.00 μ.
FIG. 158. Syrian Dassie (*Procavia syriacus*), 31.00 μ.
FIG. 159. Dugong (*Dugong dugong*), 1177.00 μ.
FIG. 160. Hair Seal (*Otaria jubata*), 105.00 μ.
FIG. 161. Indian Elephant (*Elephas indicus*), 200.00 μ.
FIG. 162. Coendou (*Cœndou mexicanus*), 38.00 μ.
FIG. 163. Antarctic Seal (*Hydrurga leptonyx*), 185.00 μ.
FIG. 164. Vicuna (*Lama vicuna*), 11.00 μ.
FIG. 165. Malayan Pangolin (*Manis javanica*), 290.00 μ.
FIG. 166. Mammoth (*Elephas primigenius*), from Alaska, 50.00 μ.

[5] The fur hair of many species of mammals varies upon different parts of the body, sometimes with respect to the configuration of the scales and medulla. Hence samples for comparison must be taken, as far as possible, from the same regions.



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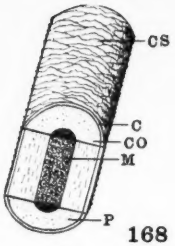

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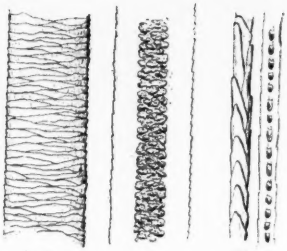

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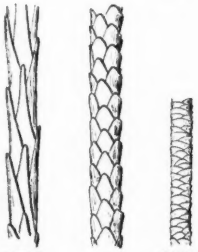

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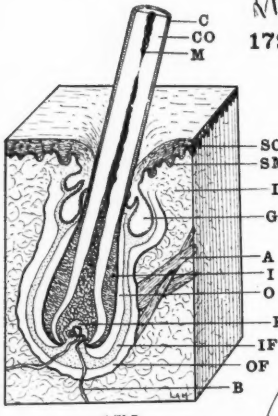

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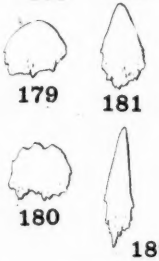

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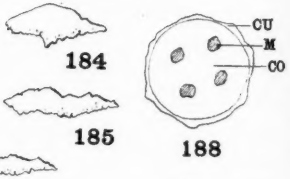

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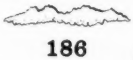

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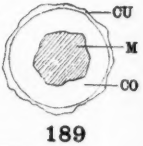

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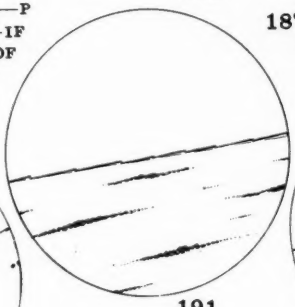

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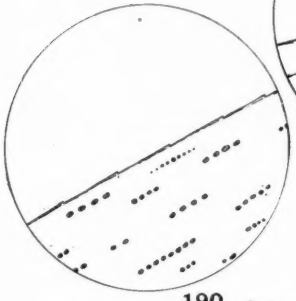

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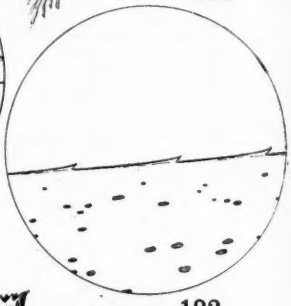

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EXPLANATION OF PLATE VII

FIG. 167. Longitudinal section through an ideal generalized mammalian hair, of the discontinuous medulla variety, to show the relation of its structural elements.

CU, cuticle,
CO, cortex,
MC, medullary cell or chamber,
I, interstitial medullary space,
MS, medullary shaft or column,
FCU, free ectal edge of cuticular scale,
P, pigment granules.

FIG. 168. Stereogram of ideal generalized mammalian hair of the continuous medulla variety.

CS, cuticular scales,
C, cuticle,
CO, cortex
M, medulla,
P, pigment granules.

FIG. 169. Protective hair of European Beaver (*Castor fiber*) to show cuticular scales.

FIG. 170. Protective hair of European Beaver (*Castor fiber*) to show medulla.

FIG. 171. Fur hair of European Beaver (*Castor fiber*).

FIG. 172. Fur hair of Platypus (*Ornithorhynchus anatinus*) just above the mouth of the follicle.

FIG. 173. Fur hair of Platypus (*Ornithorhynchus anatinus*) one third of the distance from the base to the tip.

FIG. 174. Fur hair of Platypus (*Ornithorhynchus anatinus*) near the distal extremity, or tip.

FIG. 175. Protective hair of Skunk (*Mephitis mephitica*) to show cuticular scales.

FIG. 176. Protective hair of Skunk (*Mephitis mephitica*) to show medulla.

FIG. 177. Fur hair of Skunk (*Mephitis mephitica*).

FIG. 178. Stereogram of an ideal generalized mammal hair in its follicle.

C, cuticle,
CO, cortex,
M, medulla,
SC, stratum corneum of epidermis,
SM, stratum malphigii of epidermis,
D, dermis, corium,
G, sebaceous gland,
A, muscles which erect the hair shaft,
I, inner layer of root sheath,
O, outer layer of root sheath,
P, papilla,
IF, inner layer of follicle,
OF, outer layer of follicle,
B, blood and nerve supply to the bulb of the hair.

FIGS. 179 to 186. Various types of imbricate scales (referred to in text).

FIG. 187. Hair shaft showing teased-out cortical element.

CO, cortical cells or hair spindles.

FIG. 188. Transverse section through hair with compound medulla.

CU, cuticle,
M, medulla,
CO, cortex.

FIG. 189. Transverse through a hair with simple or single medulla.

CU, cuticle,
M, medulla,
CO, cortex.

FIG. 190. Portion of shaft of fur hair of Mandril (*Cyanocephalus maimon*) to show the configuration and disposition of the pigment granules.

FIG. 191. Portion of the shaft of the protective hair of the Badger (*Taxidea americana*) to show the configuration and disposition of the pigment granules.

FIG. 192. Portion of the shaft for the fur hair of Wolverine (*Gulo luscus*) to show the configuration and disposition of the pigment granules.

FIGS. 193 to 199. Various types of corneal scales (referred to in text).

under examination, since the form of the scale (more especially) undergoes alteration from the base to the tip of the hair shaft. As a rule the scales at the base of the hair are of greater longitudinal than transverse diameter, while the converse is true of the scales at the tip of the shaft. Figs. 172, 173 and 174 illustrate the nature of the change in form which is normally met with in the hairs of mammals as it occurs in the fur hair of the platypus (*Ornithorhynchus anatinus*). This modification in the form of the scales is believed to be due to the increasing amount of wear to which the hair shaft is subjected the farther away it is pushed from the follicle. That external friction is the cause of scale alteration in form is likewise suggested by the fact that the stiffest hairs possess, usually, scales of a much flattened type (cf. Figs. 57 to 67, inc.), while the finer hairs show the delicate, free ectal edges of the scales unchanged for at least the proximal three fourths of the length of the shaft. This is especially well illustrated in the hair of the bats, notably in such species as the mastiff bat (*Molossus sinaloæ*) (Fig. 105); the wrinkled-lipped bat (*Nyctinomus bocagei*) (Fig. 106); and the intermediate bat (*Mormops intermedia*) (Fig. 107).

The fur hairs shown in the plates[6] were chosen with the view of bringing out most clearly the nature of the forms of the simple varieties of scales and medullas, and of their various common modifications, as they exist one third of the distance from the mouth of the follicle to the top of the hair shaft. For convenience, therefore, the scales and medulla in this portion of the hair shaft have been termed *mature scales* and *mature medulla.* The scales at the distal extremity of the hair shaft, whose modification in form is considered to be the result of attrition, are called the *attritional scales,* and the pinched out medulla of the same region, the *fragmentary medulla.*

Inasmuch as the hair shafts represented in the plates

[6] The fur hair shown in the plates were taken, where possible, from the region of the median line of the dorsum, just below, *i.e.*, caudad of, the shoulders.

vary so widely in diameter (6.80 μ in the hair of the intermediate bat (*Mormops intermedia*) (Fig. 107); and 1,177 μ in the hair of the dugong (*Dugong dugong*) (Fig. 159), to draw them to the same scale, and at the same time to make the smaller hairs of sufficient size to show clearly the cuticular scales and medullas, was obviously impracticable. The arbitrary expedient was therefore adopted of drawing all the hairs whose diameters were equal to, or less than, 50 μ to one size, and drawing all those hairs whose diameters were greater than 50 μ to another size. In the figures the latter hairs are represented as being slightly greater in diameter. Such a division into coarse and fine hairs is not without its basis in common use, for it was found that as hairs are greater or less than 50 μ in diameter they are called respectively coarse or fine, or stiff and soft, by perhaps the majority of persons. The true spines form still a third division, with which, however, we shall have nothing to do.

Such an arbitrary representation of hair shafts, however, affords no appreciation of the relative or actual magnitudes of the hairs. In order that this might be had, therefore, the actual diameter of the fur hair of each species, in micra, is given after the name in the explanation of the plates. In each case this, obviously, is approximate only, the result of averaging a large number of individual measurements. It was found that the diameters of the hair shafts of any given individual vary considerably, and that a somewhat less range of variation occurs among the averages of different individuals of the same species. Hence it is inferred that only a meager amount of significance should be attached to hair magnitudes, except possibly, in large averages, and between large groups, *i.e.*, families or genera.

It must also be borne in mind that the prepared hair shaft, underneath the microscope, does not reveal at any one time the complete contour of the cuticular scales, or medulla, as it is represented in the figures. This is due to the fact, that with the objectives of sufficiently high

power to resolve the scale outlines, or the structure of the medulla, but one portion of the cylindrical hair shaft can be brought into exact focus at a time. The objective must in focusing *follow around the hair,* as it were, up one side, and down the other, revealing, as it goes, the course of the outline of the scale, or of the irregularities of the medulla. The resulting curves are then drawn on the single plane of the paper, as though the hair had, by some means, been crushed out flat without distorting its structure. It is because of this rotundity of the various elements of the hair shafts that it is often impossible to secure adequate photomicrographs of hair shafts, since it is necessary to employ high-powered objectives with a consequent very limited foeal depth. Moreover the various different indices of light refraction and reflection among the hyaline elements of the shaft produce, upon the finished photograph, various striations and markings of one sort and another, which have no analogue in the actual structure of the hair shaft itself. It is possible, however, that photomicrographs of small, highly magnified portions of the hair shaft, cortex may be very useful in determining the form and placentation pattern of the pigment granules.

The figures of the fur hairs are arranged with the simple form of each type of scale, or medulla, coming first, followed by its various common variations. The hair of the civet (*Arctogalidia fusca*) (Fig. 1) represents the simplest form of the imbricate scale, termed the ovate. Fig. 179 shows the normal appearance of a single isolated scale of this type. Figs. 2 to 7 show the commonest modifications which the ovate scale undergoes. Of all of the imbricate scales whose longitudinal axis is equal to, or greater than, the transverse axis, the ovate is the most common.

Between the ovate scale and the acuminate, no definite line of demarcation can be drawn. I have considered Figs. 8 and 9 to represent perhaps the simplest form of the acuminate type. Figs. 10 to 17 show scales of in-

creasing acuminateness, while Figs. 18 to 20 show curious anomalous varieties.

In Figs. 181 and 182 are shown two isolated acuminate scales of characteristic outline.

The elongate type of cuticular scale (Figs. 21 to 35) is one least often met with, especially in its typical form, as shown in Figs. 29 to 31. The simplest variety (Fig. 21) possesses a longitudinal axis only a trifle greater than the transverse one. Figs. 29 to 31 are the typical varieties, and Figs. 32 to 35 show forms difficult to group. They are, however, tentatively put with the elongate forms. A single dissociated elongated scale is shown in Fig. 183.

By far the commonest types of scale which one encounters are the crenate and flattened types. The former are illustrated by Figs. 36 to 67. In this form of scale the transverse axis is much greater than the longitudinal, and the free ectal, or outermost edge of the scale is irregularly waved or crenulated. Of this type, a confusing multiplicity of variations occur. Some of the plainest and most easily interpreted of these are shown. Fig. 36 is considered to represent the simplest form. Scales like those shown in Figs. 57 to 67 are usually associated with the hairs of the greatest diameter, *i.e.*, the coarse, or stiff hairs, or bristles. This form is also characteristic of the majority of the spines. Two typical crenate scales, dissociated from the cortex, are represented by Figs. 185 and 186.

The flattened type is equally common and differs from the crenate only in exhibiting an ectal edge smooth and comparatively free from sudden irregularities. The longitudinal axis, however, is frequently but little greater than the transverse one, as can be seen in such hairs as are represented by Figs. 69 and 70. Fig. 68 represents the simplest form, and Fig. 184 a single scale of the same type.

In the coronal scale we have a scale fundamentally different from the imbricate. Here the scale usually com-

pletely surrounds the hair. The cuticular portion of the hair may be likened to a pile of tall tumblers placed one within the other, the upper rims representing the free ectal edges of the scales. Isolated coronal scales of various types are represented in Figs. 193 to 199. Fig. 93 represents a form which may be regarded as one of the simplest of the coronal scales. An isolated scale of this form is also shown in Fig. 193. The numerous variations of this type of scale are usually in the direction of a more flaring and more irregular ectal edge, as can be seen by comparing Figs. 93 to 113, and Figs. 193 to 199.

The coronal scales may be subdivided into simple (Figs. 93 to 102), serrate (Figs. 103 to 107), and dentate (Figs. 108 to 113). The simple scales, as well as the serrate are the forms usually found among the bats, which are fairly constant in this regard. Figs. 106 and 107 represent, perhaps, the maximum of scale decoration among the mammals. These scales, isolated from the cortex, are shown in Figs. 196 and 197. The intermediate bat (*Mormops intermedia*) whose hair is illustrated by Figs. 107 and 197, possesses, possibly, the finest of mammalian hair. The shafts of the fur hair average 6.80 μ in diameter, and often shafts of as small a diameter as 4.30 μ can be found. In these hairs, apparently, the cuticle has become greatly thickened, and the medulla has been lost. This seems to be true of the majority of the bats, more particularly of those bearing the serrate type of cuticular scales. The dentate type of scale is not found among bats, but seems to be scattered among several orders of mammals. It occurs most frequently among the members of the glires, or rodents. The simplest form is shown in Fig. 108, and other typical forms in Figs. 109 to 112. There seems to be not a great range of variation in this type of scale, the majority of species which bear this type of hair approximating very closely to the forms shown in Figs. 109 to 112. Fig. 113, however, shows an anomalous form of scale characteristic of both the American and European species of otter. In

this form the scale reaches its greatest length, as can be seen by the isolated scale, Fig. 198. The shorter scale, of the usual dentate type is shown in Fig. 199.

Of the three great groups of medullas: the discontinuous, the continuous, and the fragmental, the first seems to be subject to the greatest range of modification. This has been subdivided into simple, and compound types. The simple, furthermore, can be grouped as: ovate, represented by Figs. 114 to 126, elongate, shown by Figs. 127 to 128, and flattened, illustrated in Figs. 129 to 135.

The ovate type, in its various modifications, is met with usually, in hairs of small diameter. Thus the hairs of the shrews, moles, small rodents, one or two bats, etc., possess hairs of ovate medullas. The form usually encountered is apt to be more nearly like those shown by Figs. 114 to 118, than like the remainder of the ovate types (Figs. 119 to 126). The latter, especially such partially fused forms as shown in Figs. 120 and 121, are infrequently seen.

Still less common than these forms are the forms of the elongate medullas (Figs. 127 to 128). These must not be confused with the various fragmental types (Figs. 155 to 166). In the latter the divisions do not represent regularly placed cells or chambers as in the former.

The compound medullas, at least in the fur hairs, are the least common of all. Two varieties can be easily distinguished; the cells of one being ovate (Fig. 136), and the cells of the other flattened (Fig. 137). No instances of elongate cells were observed.

The continuous medulla (Figs. 138 to 153) seems to be the one characteristic of more than half of mammal hairs, particularly of those which are greater than 50 μ in diameter. It is found in nearly all of the protective, or over hairs, and is present in all spines and bristles, in some portion of the shaft. Fig. 168 shows a hair of this type as it would appear if sectioned to show the longitudinal and transverse appearance of the continuous medulla. The whole interior of the medullary column or

shaft (*MS*, Fig. 167) is filled with an anastomosing mass of cornified filaments, which probably represent a closely compressed aggregation of small medullary cells (Fig. 178). A type of medulla in which the component cells are still preserved so that their individual nature can still be seen, is shown in Fig. 147. Two divisions of the continuous medulla can be readily recognized; the nodose (or irregular) (Figs. 138 to 147), and the homogeneous Figs. 148 to 153). Between these two forms, all sorts of intergradational varieties exist.

The fragmental medulla (Figs. 155 to 166) represents perhaps various stages in the reduction of this element of the hair shaft structure, and seems to have been derived from the continuous type. Where the medulla seems to be lacking altogether, minute traces can still be found in various portions of the hair shaft, particularly in the region just below the mouth of the follicle. Structural indications seem to suggest that the development of medullas is from the discontinuous, through the continuous, to the fragmental, and finally, as is the case in the bats, to no medulla at all.

To prepare hairs for microscopical examination care must be exercised that the reagents used in cleaning, staining, etc., do not soften the cuticle, and thus distort the form of the scales, or that the cover glass is not made to press too heavily upon the hair, and thus flatten it out, deforming both the cuticular scales and medulla as well.

The simplest treatment for scale examination consists in washing the hair thoroughly in a solution composed of equal parts of 95 per cent. alcohol and ether (or chloroform). The hair may then be dipped into pure ether, or chloroform, to insure rapid drying, and when thoroughly dry placed upon a slide and covered with a cover glass for immediate examination. Some hairs, *e.g.*, those of sheep of most varieties, the fur hair of the camels, and the protective hair of many of the bats, notably the silvery bat (*Lasionycteris noctivagans*), exhibit the scales very well after this simple treatment. The 8x or 10x eye-

piece, and the 4 mm. objective with transmitted light, preferably from a blued glass, or better, daylight glass, gives the best results. Indirect lighting, with the mirror swung to one side, may be used where the scale edges are not easily seen. Reflected light has been found excellent, but only in a very few cases.

With hairs like those of the rabbits and hares, shrews, moles, the fur hair of bats, and the like other manipulations of the hair must be brought into requisition. One of the most generally useful of the various staining preparations consists in immersing the hair, after its ether-alcohol bath, in a solution of gentian violet, methyl blue, methyl green, or safranin, in 95 per cent. alcohol. The stain is prepared by making up a saturated solution of the stains enumerated, and then diluting each with 95 per cent. alcohol to the desired degree of color depth, which must be empirically determined for each different species[7] of hair. The evaporation of the alcohol, which must be accomplished rapidly in a warm current of air from a bunsen flame, deposits in the depressions just ectad of each cuticular scale edge, a tiny bit of the stain, which therefore clearly outlines the contour of each individual scale. This method is difficult, and the writer has found that repeated trials with the same hairs were frequently necessary before satisfactory results were secured. In working with hairs it is better to use a tuft of 25 or 50, rather than try to work with but a few.

The preparation of the hair, is, however, of but slight importance compared with the manipulation of the proper lighting and the proper combination of objective and ocular. Where the cuticular scales remain obstinately invisible, or only faintly seen, various sorts of illumination must be tried; transmitted vertical light, transmitted oblique light, dark field illumination, reflected light, and polarized light. Dark field illumination,

[7] The writer is aware that "species of hair" is hardly admissible, yet the convenience must be the excuse for its use.

with the 1.8 mm. objective and 4x eyepiece was found excellent for a large number of hairs. It must be borne in mind that, in using this combination of immersion objective with the dark field illuminator, an oil connection must also be formed between the upper surface of the condenser and the lower surface of the slide.[8] Exigency of space forbids the descriptions of the various types of lighting which have been found most satisfactory with the various species of hairs. These must be empirically determined by each investigator. The degree of success obtained with the microscope usually depends as much upon the preparation of the instrument and its lighting, as upon the preparation of what is to go under it for examination.

For examination of the medulla all that has been said regarding lighting, etc., applies. However, the various treatments given the hair and used to render visible the cuticular scales, obscure the medulla. The simplest and most generally useful method of rendering the medulla clear, consists in reducing the visibility of the cuticular scales to as near zero as possible by mounting the hair, beneath the cover glass, in some light microscopical oil, such as oil of bergamot, of cedar, or origanum, of amber, of cloves, etc., after having washed it, as before, in the ether-alcohol solution. Such a treatment renders the hair, in effect, a glassy cylinder, within which the medulla can be clearly seen, provided the cortex is not thickly besprinkled with pigment granules, or rendered dark in color by diffuse pigment. Fortunately most of the fur hairs are lightly pigmented. Many of the protective hairs, however, are so heavily colored that the medulla is partially, or almost wholly, obscured.

Some of the finer hairs can be examined with advantage in a mount of clear water, or xylol. The best treat-

[8] For directions for all sorts of microscope manipulations, apparatus, microscopical principles, etc., consult Professor S. H. Gage's comprehensive "The Microscope, and Introduction to Microscopic Methods and to Histology," Ithaca, N. Y., 1917. A new edition of this valuable work is now ready to leave the press.

ment, however, was found to consist in washing the hair in the ether-alcohol, drying, immersing in xylol, and then mounting in very thin Canada balsam. This makes a permanent mount.

Lighting with the dark ground illumination was found to give the best results in the examination of the external configuration of the medulla.

In the case of hairs where the heaviness of the pigmentation obscures the medulla, or in compound-medullated hairs, or in those cases where an accurate knowledge of the form of the cross section of the medullary column is desired, it is necessary to prepare cross sections of the hair shaft, by the usual methods of imbedding in paraffin or celloidin.[9] Figs. 188 and 189 show the manner in which the form of the medulla is shown in transverse sections, as well as its relations to the thickness of the cortex and of the cuticle.

The methods used to make clear the medulla serve well also to reveal the pigment granules. In examination of the shaft for these tiny bodies the 1.8 mm. objective and the 10x eyepiece with the draw tube of the microscope extended its full length was found to be the lowest power which could be satisfactorily employed. Lighting with daylight glass and a 200-watt tungsten-filled bulb was apparently a necessity.

The cortex, because of its nearly homogeneous structure, was not found to exhibit characters which could be used as criteria for identification. Fig. 187 shows a hair macerated in caustic soda, and with the cortex teased out to show the distorted, elongated cortical cells, or hair spindles.

The use of caustics and strong acids for dissociating the cuticular scales is not recommended. The softening of the scales distorts their form and thus renders them useless for delicate determinative purposes.

It very often becomes necessary to distinguish the dis-

[9] For histological methods consult Professor M. F. Guyer's "Animal Micrology," Chicago.

tal from the proximal end of some one hair shaft. This can be done under the microscope, remembering: first that the image is reversed, and second, that the free edges of the cuticular scales lie always at the ectal, or distal portion of the scale, and so indicate the direction of the distal extremity of the hair. A much more simple method is to rub the hair in question between the thumb and finger, when it will always travel in the direction of the bulb, *i.e.*, in the direction of its proximal extremity. This fact that the free ectal edges of the cuticular scales develop in such a way that they are always directed outward from the animal, suggests that they may afford protection against the intrusion between the hairs, and so on to the skin itself, of foreign bodies, parasites, and water. Furthermore any such extraneous elements which may have gained entrance, apparently would tend to be worked outward away from the skin to the outer surface of the hair covering by the motions into which the hair is thrown by the movement of the muscles of the body during locomotion.

In preparing a series of animal hairs to be used as type specimens for determinative comparisons with unknown hairs it is well to have a series of slides prepared to show the medulla (mounted in balsam as previously directed), and another series of slides with the hairs mounted thereupon in dry cells[9] (washed in the ether-alcohol, and stained or not as each requires), to show the cuticular scales. Since this later method of preparing hairs seems to be attained with little success (too much dust gathering upon the hair, the fibers obscuring the sculpturings of the cuticular scales), it is better, perhaps, to keep a tuft of each species of hair in a small phial or double envelope, and make fresh preparations when necessary. Both the balsam-mounted slides and the untreated hair samples should be filed away following the classification scheme for the scales and medulla given in this paper. This facilitates the immediate selection of the particular group of hairs possessing the charac-

teristics of the unknown sample, and makes identification much easier and quicker. For each species of mammal samples of the hair from several regions of the body should be had, as well as samples of both the fur and protective hairs of various regions. From his own experience, however, the writer is well aware that this is an ideal more easily recommended than realized.

THE EFFECT UPON THE WHITE RAT OF CONTINUED BODILY ROTATION

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EVERYONE knows that a rapid turning-about upon the heels usually leads to dizziness and that a like state is induced in the revolving chair or the turn-table of the laboratory or in the merry-go-round of street fairs. It is also known, especially among those who have attempted to analyze the complicated experience of dizziness, that an important constituent of this disturbed state of mind and body is a characteristic movement, to-and-fro, of the eyes. To this ocular twitching, which is sometimes called "nystagmus," is due, in large measure, the apparent swimming movement of surrounding objects. The twitching appears soon after rotation begins and it continues, with characteristic modifications, for a short period after the body comes to rest.

The bodily and mental effects of rotation in man and in other animals have for a good many years been made the subject of investigation by physicists, anatomists, physiologists, psychologists and medical men. It is supposed that rotation produces a specific effect upon the neural end-organs of the semicircular canals, and it is definitely known that, in addition, pretty much the entire organism is involved in the general disturbance. Concerning the ocular movements themselves, a good deal has been learned. We know, for example, that the character and the duration of the nystagmus depend upon a large and heterogeneous group of conditions, among which may be named the general state of the organism, the state of attention, the associative connections, the rate, regularity and duration of the rotational movements, repetition and practise, and other mental and physical conditions. Of

these conditions, we are here concerned with one only, *i. e.*, with the effect of regular and continued repetition upon the ocular movements in question.

It has been commonly observed that long persistence in whirling movements may reduce in intensity the distressing symptoms of dizziness. This reduction under repetition has suggested that the accompanying ocular movements may also tend, under persistent practise, to disappear. The testimony of whirling dancers and gymnasts, who are frequently undisturbed by the swimming and the giddiness, points in this direction,[1] and further evidence, of an experimental sort,[2] has recently been derived from subjects who were rotated about three minutes daily for two or three weeks. At the end of this period the subjects had lost, either wholly or in part, the "after-nystagmus" which usually persists, as we have seen, when the body has come to rest.

Now these experimental results have been sharply criticized by two otologists, Drs. Fisher and Babcock,[3] who are distressed that the stability of such a "reflex reaction" as nystagmus should be called in question. "Clinical medicine has," as they observe, "for years relied upon the permanency and the constancy of reflex phenomena." As for the results just referred to, they set them down as "pathological." Professing to repeat the experiments, but wholly missing the essential point of the method which they criticize, these men have come, not unnaturally, to a conclusion which is not antagonistic to the dogma of the invariable reflex. Despite the miscarriage of their method, however, they do find a certain amount of reduction in time of nystagmus and this reduction they propose to explain by the voluntary "gaze-fixing" of "a few subjects." Although the abortive

[1] Parsons, R. P., and Segar, L. H., "A Correlation Study of Bárány Chair Tests and Flying Ability of One Hundred Navy Aviators," *J. Amer. Med. Ass.*, 1918, 70, 1064.

[2] *Manual of Medical Research Laboratory*, Washington, D. C., 1918, 186 ff.

[3] Fisher, L., and Babcock, H. L., "The Reliability of the Nystagmus Test," *J. Amer. Med. Ass.*, 1919, 72, 779 ff.

attempt of Fisher and Babcock affords no positive evidence against the demonstrated reduction of nystagmus under repetition,[4] it has suggested an *experimentum crucis* which is designed to show that the reduction is *not* an artefact produced by the "wilful gaze-fixing" of inconvenient subjects who acquired "the art of holding the eye more or less fixed voluntarily" upon a "distant object."

We have chosen the white rat as a subject in our crucial experiment. The rat is admirably adapted to this sort of problem. It is docile and easy to handle. The lack of a fovea and of distant vision and the probable absence of all clear-cut retinal images[5] seem to provide the optimal conditions of non-fixation as suggested by the otologists' contentions. On the other hand, the pupil of the rat's eye is easily observed, as well as those portions of the sclerotic coat which project beyond the surrounding cutaneous and hairy tissues.

The following method of rotation and observation was employed. Upon a pivoted wooden platform, 11 cm. $\times$ 20 cm., was set a glass bell-jar 11 cm. in diameter and 12 cm. in height. The rat was so placed under the glass jar that its center of gravity lay over the center of rotation. A small motor, governed by means of a friction-brake, served to provide a very regular and easily controlled means of rotating the platform and the jar. Records of the time of after-nystagmus were at first made with a stop-watch, but later with a key connected to an electric signal-marker which registered on a revolving smoked

[4] As a matter of fact, these authors unwittingly furnish the most delicate and unimpeachable evidence *for* the very reduction which they deny. Although they apparently omitted to repeat at each sitting, giving each of the ten subjects included in their Table II only one turning to the right and one to the left, *in every single case the average nystagmus-time is less for the second five days than for the first five days.* That is to say that a *single turning* each day (not a series) is sufficient to reduce the time for subsequent days. The tendency to reduction must, then, be much greater than the first experimenters had contended or supposed.

[5] Vincent, S. B., "The Mammalian Eye," *J. of Animal Behavior*, 1912, 2, 249–255. See table and also references to the literature.

drum.[6] It was found, by preliminary trials, that the appearance of the nystagmus was directly proportional to the *number* of rotations and to the *speed* of rotation. For experimental purposes, an arbitrary choice was made of a speed of ten revolutions in fifteen seconds. Ten trials of ten rotations each were repeated two or three times a day, save for subjects "I" and "J," which were given twenty trials twice a day. The subjects were ten white rats, five males and five females, all about three months old. The functional integrity of the mechanisms of equilibrium[7] was roughly determined by observing the rats' behavior under daily conditions of life, and by throwing them into the air and dropping them. All of the subjects responded quickly and positively to such tests. In the subsequent experiments each rat was rotated a like number of times to the right and to the left, and averages of the duration (in seconds) of the nystagmus after stopping were computed. A comparison of these averages from day to day may be made from Table I.

The outstanding feature of the investigation is the rapid decrease of after-nystagmus from day to day, as is clearly indicated in Table I. Within ten to eighteen periods of rotation the nystagmus had completely disappeared. The number of ocular movements after stopping the platform was also observed. Upon the first rotation for each rat, the number of movements varied between 18 and 25. This number rapidly decreased during the first four or five periods to between 5 and 8, and soon became reduced to a single movement which generally hung on for some time. As the rotation was stopped, the eye gradually moved in the direction of the preceding rotation and then jerked back to normal position. The

[6] This latter method was used by the Psychological Department of the Mineola Research Laboratory. It is a decided improvement over the clinical method of observation by the stop watch. See "Manual," p. 190.

[7] The semicircular canals of Rodentia are well developed and quite regular in form. See Gray, A. A., "The Labyrinth of Animals," 1907, Vol. I, pp. 165 ff.

TABLE I

Subject.....		A		B		C		D		E		F		G		H		I		J	
Direction of Rotation		L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
Number of series	1	6.70	7.04	5.88	6.06	5.00	5.80	5.80	6.40	5.34	5.06	6.02	4.82	4.40	4.60	5.80	4.60	5.66	5.86	5.12	6.16
	2	5.62	5.80	4.52	4.90	4.96	4.60	5.32	5.20	4.76	4.02	4.20	5.12	4.60	4.60	6.00	5.00	4.35	4.45	3.96	4.06
	3	4.32	4.32	4.02	4.18	4.08	4.44	4.60	4.72	4.22	3.20	3.56	3.66	3.80	3.64	4.46	5.30	4.10	3.95	3.82	3.58
	4	3.78	4.10	3.70	3.76	3.26	3.92	4.08	4.20	2.58	1.80	3.56	2.64	4.78	4.30	3.88	4.04	3.00	2.98	3.72	3.30
	5	3.22	3.48	3.48	3.42	2.96	2.30	2.96	3.00	2.88	2.56	3.06	2.42	5.46	5.20	3.92	4.54	2.10	2.20	3.52	3.96
	6	2.68	2.62	2.70	2.58	1.28	1.28	1.78	1.96	1.50	1.36	1.28	1.50	4.46	4.34	4.20	4.64	1.18	1.56	2.74	2.94
	7	2.06	2.18	2.34	2.26	1.00	1.00	1.08	1.06	1.32	1.08	1.02	1.04	4.46	4.76	3.68	5.16	0.96	1.18	2.86	3.42
	8	1.62	1.74	1.74	1.80	0.60	0.60	1.00	1.00	0.60	0.86	1.00	1.00	4.18	3.68	3.58	3.18	0.40	0.50	2.96	2.92
	9	1.32	1.48	1.54	1.56	0.20	0.20	0.40	0.40	0.20	0.20	0.40	0.40	4.18	3.96	4.58	4.14	0.50	0.20	2.60	2.70
	10	1.04	1.56	1.26	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.20	3.54	3.34	3.82	3.86	0.00	0.00	2.14	2.56
	11	1.00	1.00	1.22	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.72	3.58	2.96	3.42	0.00	0.00	1.60	1.58
	12	0.80	0.60	0.60	0.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.66	3.76	3.10	3.40	0.00	0.00	1.76	1.38
	13	0.40	0.40	0.00	0.00									3.80	3.56	3.76	3.64			0.20	0.80
	14	0.00	0.00	0.00	0.00									3.50	3.74	3.68	3.60			0.10	0.20
	15	0.00	0.00	0.00	0.00									3.32	3.08	2.54	3.14			0.00	0.00
	16													2.24	1.84	2.16	2.18			0.00	0.00
	17													1.34	1.44	1.40	1.70				
	18													0.00	0.00	0.00	0.00				
	19													0.00	0.00	0.00	0.00				

disappearance of this one movement accounts for the sudden falling off of the time-values at the end of the various series. The average initial time of after-nystagmus for all subjects was 5.57 sec. for rotation to the left and 5.74 sec. for rotation to the right. Other averages testify to this difference in time for the two directions of rotation. This seems to be a genuine case of individual difference quite comparable to similar differences found in human observers.[8]

The fact of decrease from day to day is incontestable. Each column in Table I shows it. It is just as apparent, if, in each day's series, an average of the first two trials is taken and compared with corresponding values for subsequent days. That is, each day begins at just a little lower nystagmus-time than the preceding day began. Furthermore, the decrease is of a characteristic kind. Table I indicates that at least one half of the total decrease commonly occurs in the first few days of experimentation. The exceptions, subjects "G" and "H," will be considered later. In this respect, a "nystagmus curve" is quite comparable with the common "learning curve," save for the absence of plateaus.

Again, the figures make it plain that there is also a general decrease in the time of after-nystagmus within any single day's turning. Table II indicates that this decrease was constant for all subjects, save "G" and "H." An analysis of the material upon which the table is based shows that the main decrease within any single day falls early in the series—a result consonant with the early fall in time from day to day, as just mentioned.

It must be emphasized that any decrease is for one set of conditions only. Only those values are given which resulted when the rat rested quietly on the floor of the rotated platform. Occasionally the rat would stand almost upright, in which case the nystagmus was almost invariably longer. Even after the disappearance of the

[8] See "Manual," *passim*, and also articles in the *J. Amer. Med. Ass.*, cited above.

TABLE II

Subject	L		R	
	I	II	III	IV
A	2.81	2.49	2.84	2.51
B	2.84	2.30	2.81	2.51
C	2.74	2.31	2.74	2.66
D	3.18	2.89	3.13	3.00
E	2.59	2.48	2.50	2.02
F	2.57	2.23	2.56	2.03
G	3.46	3.50	3.40	3.30
H	3.26	3.41	3.44	3.55
I	2.98	2.18	2.93	2.23
J	2.98	2.33	3.28	2.65

Column I, averages of all the first two rotations to the left for all series; column II, the average of all the last two rotations to the left for all series; columns III and IV, the same for rotation to the right.[9]

nystagmus under *usual* conditions, this upright posture induced some after-nystagmus; but it is important to note that the time and the intensity of it were never so great (by more than half) as the original nystagmus in these positions. That is, there seems to be a "transfer" effect from one set of conditions to another. Changing the speed or the number of rotations at any time produced a similar reappearance of nystagmus, but never in its original intensity or temporal duration. Several of the subjects gave a nystagmus varying between twelve and twenty-five seconds when rotated once a second for thirty seconds before the practise series. After the practise series, these values were reduced to about the level of the original values for the rotation-rate used in the investigation, viz., 5–6 seconds. The change of position of the rat during and after rotation had to be carefully regarded; for such a change was frequently responsible for an increase of nystagmus-time that obscured a real decrease.

There are several special points of importance.

1. It has been noted above that subjects "G" and "H" offer certain exceptions to our conclusions. Table I indi-

[9] Mean variations from the averages given in the tables were computed, but since they were not of sufficient magnitude to affect the significance of the figures as given they have been omitted.

cates that the length of their total series was greater than that of any of the other rats. These two subjects were females rotated during the period of gestation. Their rotation was marked by frequent and severe retching movements, defecation, and micturition. The period of gestation of subject "G" was three days short. "G" became too sick during the last reported turning to be used further, and a day later, during which time she did not seem to recover, a litter of two were born. These coincidences point directly to the fact that nystagmus is closely related to the organic condition of the individual rotated and they at least suggest the fruitfulness of further work upon this matter.

2. The fact that the white rat is a nocturnal animal[10] suggested that the time of day might make a difference in values. Accordingly two rats, "I" and "J," were rotated twenty times twice a day, early in the morning and late in the afternoon. The results were as follows:

	I	J
Morning trials, rotation to left (ave.)	2.24	2.81
rotation to right (ave.)	2.37	3.17
Evening trials, rotation to left (ave.)	1.70	2.44
rotation to right (ave.)	1.88	2.40

The morning nystagmus is invariably longer, the difference being most pronounced early in the series. Additional evidence of this diurnal difference is being sought with both human and animal subjects.

3. Other responses than the nystagmus were scrupulously noted in our observations. During the first days, most of the subjects showed a tendency to excessive defecation and micturition. Frequently the feces were not of the solid character of normal life but were quite liquid, suggesting that the rotation had induced some sort of temporary organic shock. This supposition is supported by the facts that neither micturition nor defecation ever occurred late in the series and that the rats, although

[10] Slonaker, J. R., "The Normal Activity of the Albino Rat, etc.," *J. of Animal Behav.*, 1912, 2, 20–42.

hungry, frequently refused to eat immediately after earlier turnings, although later they eat quite readily. Other evidence of a general organic disturbance is found in the violent trembling which frequently seized some of the rats during a given series. This trembling was distinct from that behavior mentioned before which reminds one of nothing so much as the retching of nausea in human beings. I have failed to find a single case of nauseation in the rat which resulted in an esophageal discharge. The retching did not seem to occur so readily if the rat had had food before the rotational period. The trembling was by far the most characteristic performance and was common to most of the subjects. That the trembling was organically based could be determined by holding the rat just after turning. The visceral organs seemed to be convulsed. The eyes were partially closed and the vibrissæ trembled violently because of the trembling of the mouth parts. This behavior occurred for two or three days after the series had been started and in the case of some of the subjects was the last observable response to the rotation.

4. It is difficult to get a quantitative test for these or for more specifically kinesthetic responses. The only test used in this connection was an enumeration of the number of spontaneous movements made before, during, and after rotation, as the series progressed. Prior to all rotation, the exploratory movements are prominent. As rotation takes place for the first time two kinds of response are in evidence. First, the rat may make frantic efforts to move in the direction contrary to rotation so long as the platform moves. When the movement ceases the rat turns and attempts just as vigorously to move in the opposite direction. These attempts always cease in five or six seconds: they seem to reach their term with the after-nystagmus. The other characteristic response is illustrated by those subjects which squat tensely on the floor of the rotating platform with the head turned far in the direction against rotation. There seems to be a specific

inhibition of all movement and a tenseness of position leading to what one might call the "rotational posture." There is no change in the position until the end of the after-nystagmus, save that the head swings to the opposite side as rotation ceases. This second type of response can be easily induced in subjects manifesting the first kind by slightly increasing the speed of rotation. As the series proceeds, the more striking features of the rotational posture begin to drop out. The head tends to swing less and less in the direction opposite to rotation and very early the return movements—even the bringing of the head back to a straight position—disappear. Finally, the original swing itself becomes quite listless and may not occur at all provided the attention of the rat is elsewhere directed. The exploratory movements return slowly, beginning with the post-rotary period and finally entering the rotary period itself.

5. The scratch-reflex affords an excellent indication of the extensity and intensity of the bodily disturbance present during, and subsequent to, rotation. Early in a series, a scratch movement initiated before rotation is suddenly arrested as rotation begins. I have not observed any scratching during the earlier trials of a series. Subject "J" endeavored to scratch on the fourth day's rotation; but the effort was poorly localized and uncoordinated. At the end of the series, an accurately localized scratch-movement was begun and carried to completion by several subjects, and successful attempts were frequently made to cleanse the face, etc., in spite of rotation or stopping. As the exploratory movements came back to their own, the rat frequently stretched up on its hind legs. In such a position, the stopping of rotation caused a definite compensatory reaction on the part of the rat; but there was nothing here to indicate that this was more than a natural response to the effect of inertia. All of the spasmodic and uncoordinated qualities of an early event of this kind were gone. The tendency of some of the subjects to run in the direction opposite to rotation com-

pletely disappeared after a few trials. In brief, the whole series of any one of the subjects here reported displayed an increasing degree of freedom and precision of movement, as time went on. All subjects were tested for equilibration after a series had been completed and all responded to being thrown and dropped just as alertly as before rotation.

It is hazardous to draw general conclusions from an introductory study of this kind. Our problem does, however, bear directly and significantly upon the functional integrity of the equilibratory mechanisms. The facts above presented support the contention that nystagmus is closely related to the other organic responses to rotation and that it is dependent, as are these other responses, upon a large group of factors. Furthermore, we have found that after-nystagmus in the white rat decreases in intensity and duration (*a*) from day to day and (*b*) within the series of a single day. Either intensity or duration may be modified also by certain organic conditions, e. g., nausea, by speed and number of rotations, and by such general conditions as antecedent rest and fatigue. The decrease and disappearance of nystagmus are accompanied by a disappearance of the characteristic rotational posture and of other bodily disturbances, the disappearance being signalized by the reappearance of the usual exploratory movements and by such specific events as the scratch-reflex.

Fisher and Babcock tried to explain away the demonstrated loss of after-nystagmus under repetition (*a*) by charging that the human subjects were "pathological" and (*b*) by referring the observed decrease to a vicious practise acquired by "a few subjects" of "gaze-fixing" upon a "distant object." It is not clear just how their explanation can be extended to the white rats.

NOTE ON THE "PELVIC WING" IN POULTRY[1]

PROFESSOR WILLIAM A. LIPPINCOTT

KANSAS AGRICULTURAL EXPERIMENT STATION

QUITE recently Beebe (1915) proposed a four-wing theory of the origin of flight in birds in the stages succeeding the arboreal phase of their evolution. Osborn (1918) raises this theory to the position of an alternate with the older two-wing theory developed from studies on the Archæopteryx (see Heilmann, 1913). Beebe bases his theory on observations of nestlings of the white-winged dove (*Melopelia asiatica*) and the domestic pigeon (*Columba livia* Bonn.), an embryo of the jacana (*Jacana jacana*), a living specimen of the great horned owl (*Bubo virginianus*) and studies of photographs of the Berlin specimen of the Archæopteryx.

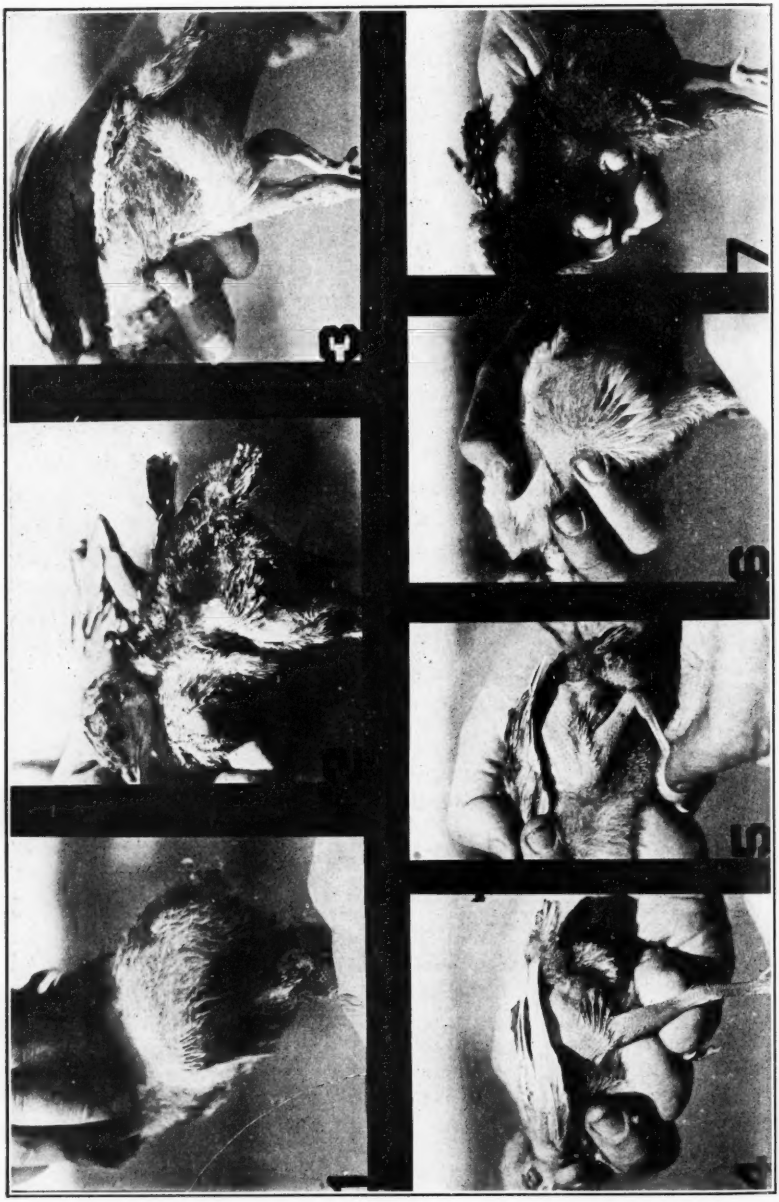
The purpose of this note is to report the presence of the structure described by Beebe, in certain domestic birds. In reporting his discovery of a "pelvic wing" in nestling birds Beebe (p. 42) makes the following statement:

> Recently while examining the fresh body of a four-days-old white-winged dove in the New York Zoological Park, I observed on its almost naked body a remarkable development of sprouting quills across the upper part of the hind-leg, and extending toward the tail across the patagium just behind the femur. A second glance showed that this was no irregular or abnormally precocious development on the part of the femoral pterylum, but a line of primary like sheaths, many of which had a very definitely placed covert.

He then proceeds to a rather detailed description of the structure which he called a "pelvic wing."

What appears to be the same structure, judging from Beebe's description and from the figures accompanying his paper, may be readily observed on most chicks of the

[1] Contribution No. 14 from the Department of Poultry Husbandry.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American and Mediterranean breeds at three weeks of age or younger and on English and Asiatic chicks a week or two later.

In the routine of describing three-weeks old chicks in connection with certain genetic studies, the writer has noted and recorded the presence of this structure on several hundred individuals. It has seldom been lacking on chicks of the Mediterranean breeds and crosses, and is usually found on chicks of the American breeds, and frequently on those of English and Asiatic breeds of this age. Its non-appearance in chicks of the lighter breeds, by the time they are three weeks old, is usually associated with low vitality and general slowness of feathering. The heavier breeds are naturally slower in passing from the down to the feather stage and its failure to develop in the first three weeks is more frequent.

While not all of the individuals which failed to show the so-called pelvic wing in three weeks were reexamined, many of them were and in every instance the structure was found at some stage of development. The parents of the chicks observed were not only of several distinct breeds and classes but were frequently from widely separated sections of the country. The number of observations made and the various sources of the breeding stock seem to warrant the belief that the "pelvic wing" in the young domestic fowl is of fairly constant occurrence.

It is interesting to note in this connection that the

EXPLANATION OF PLATE I

FIG. 1. Pelvic wing of Rhode Island Red chick hatched February 4, 1919, photographed March 27, 1919. Age fifty-one days.

FIG. 2. Pelvic wing of bronze poult hatched June 7, 1919, photographed July 11, 1919. Age thirty-four days. Some down feathers plucked to show structure more clearly.

FIG. 3. Pelvic wing of Blue Andalusian chick hatched February 25, 1919, photographed March 27, 1919. Age thirty days.

FIG. 4. Pelvic wing of Blue Andalusian chick hatched March 18, 1919, photographed March 31, 1919. Age thirteen days. Down plucked to show structure more clearly. Leg extended.

FIG. 5. The same individual shown in 4, with leg flexed.

FIG. 6. Pelvic wing of White Plymouth Rock chick hatched March 4, 1919, photographed March 27, 1919. Age twenty-three days.

FIG. 7. Pelvic wing of Barred Plymouth Rock chick hatched March 4, 1919, photographed March 27, 1919. Age twenty-three days.

"pelvic wing" is clearly illustrated in two photographic figures of four weeks old White Leghorn chicks in Rice, Nixon and Roger's (1908, pp. 25–26, Figs. 6 and 7) paper on "The Molting of Fowls." The structure is referred to by these writers as "the thigh tract."

In chickens the "pelvic wing" occurs along the postero-ventral border of the femoral or lumbar tract, as described by Nitzsch (1867, Plate VII, Fig. 6) for *Gallus bankiva* and appears to be a part of it. In its development it is synchronous with, or slightly preceded by, the feathers of the humeral tract and has so much in common with the latter as to suggest that the two tracts may be homologous structures of the hind and fore-limbs, respectively. The "pelvic wing" extends across the upper part of the hind limb and a more or less well-marked patagium just behind the femur. The humeral tract extends across the upper part of the fore limb and the patagium behind the humerus.

The appearance of the "pelvic wing" of chicks of different breeds is shown in Plate I, Figs. 1, 3, 4, 5, 6, and 7.

The structure in the Bronze turkey (Fig. 2) is essentially the same as in chickens. This breed is the largest and commonest variety of domestic turkeys and most nearly resembles their native wild progenitors.

In the waterfowl the structure has not been found. This was perhaps to be expected from the figures of Nitzsch (1867, Plate X, Figs. 5, 6, and 7). The birds observed were domesticated Mallard ducks and White Embden geese. In neither could any feathers be discovered which were set off from the others of the femoral tract, either in size, or precocity of development. There is however in both species a group of feathers whose development is simultaneous with that of the feathers of the humeral tract. These are situated on a branch of the inferior tract which extends beyond the breast along the sides of the trunk almost to the knee. The feathers of both these tracts precede the remiges in development.

Nitzsch (1867, p. 146) makes note of the fact that "this

short outer branch (of the inferior tract), and the broad, obtuse axillary tract, constitute the strongest portion of the entire plumage of the trunk." The position of these feathers is such as to suggest a pelvic wing to a casual observer. He further (p. 177) calls attention to the unusual development of this branch in *Crypturus,* where it "passes through the lateral space of the trunk and unites with the extremity of the lumbar tract of the same side."

The conditions found in *Crypturus* (see Nitzsch's Plate VII, Figs. 11 and 12), ducks, geese and chickens might suggest the possibility that the "pelvic wing" in the chicken, and the branch of the inferior tract in the duck and goose are both vestiges of what was once a continuous row of rather large feathers extending from below the shoulder along the edge of the breast and out over the thigh. Such a suggestion, however, presents difficulties if the homology of the pelvic wing and the humeral tract is seriously considered. Judging from Nitzsch's figures of *Crypturus* (Plate VII, Figs. 11 and 12), there is probably no connection between this branch and the humeral tract.

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SHORTER ARTICLES AND DISCUSSION

ON THE NUMERICAL EXPRESSION OF THE DEGREE OF INBREEDING AND RELATIONSHIP IN A PEDIGREE[1]

DR. RAYMOND PEARL has given in a series of papers ("Studies on Inbreeding," I–VIII) published in the AMERICAN NATURALIST during the years 1913 to 1917 a system of measuring numerically the degree of inbreeding and relationship in a pedigree.

It will not be necessary to describe the method in any length as it may be familiar to most readers or can easily be found in the original papers.

The starting point is the fact, that all inbred individuals, notwithstanding the special system of inbreeding involved, have fewer different ancestors in a certain generation than the greatest possible number.

The degree of inbreeding is measured by the extent of this reduction in numbers of different ancestors. For that purpose a *coefficient of inbreeding* is determined for each generation according to the formula

$$Z_n = \frac{100(p_{n+1} - q_{n+1})}{p_{n+1}},$$

where p_{n+1} indicates the greatest possible number of different ancestors in the $n+1$st generation and q_{n+1} means the actual number of different ancestors in the same generation.

Plotting the series of values obtained for Z over a base indicating the series of generations, the *inbreeding curve* can be drawn. Maximum values for the coefficient of inbreeding are obtained when continuous brother and sister mating is involved. The brother and sister inbreeding curve has therefore the importance as the limit, which no other inbreeding curve can surpass.

The proportion of the actual inbreeding during a number of generations to the highest possible inbreeding in the same number of generations then offers a fairly good measure for the

[1] Papers from the Department of Biometry and Vital Statistics, School of Hygiene and Public Health, Johns Hopkins University, No. 12.

total inbreeding. This proportion can be found by determining the proportion of the area included by the actual inbreeding curve in percentage of the area included by the maximum inbreeding curve. The area of the latter can be calculated by integration. The actual curve is usually so irregular that no integration is possible. To get an approximate value the series of values for Z is simply summed. The formula for the *total inbreeding coefficient* is then the following:

$$Z_{Tn} = \frac{100\Sigma \frac{Zn}{Zl}}{F_{Tn}},$$

the Σ denoting the summation of all values between and including the limits indicated, and F_{Tn} is the area included by the maximum curve, the same number of generations being involved.[2]

A question of considerable genetic bearing is the degree of relationship between the parents of the individual, whose pedigree is being examined. Relationship is indicated by the reappearance of individuals from the pedigree of one individual in the ancestry of another.

As a measure of degrees of relationship Pearl proposed a *coefficient of relationship*. This is calculated in two slightly different ways according to whether it is measured with the coefficient of inbreeding, where the relationship of the sire and dam of the inbred individual is being calculated, or separately, when relationship of any two individuals is measured. The formulæ are as follows:

$$(1) \qquad K_n = \frac{100(p_{n+1} - q_{n+1}) - ({}_sZ_{n-1} \cdot {}_sp_n + {}_dZ_{n-1} \cdot {}_dp_n}{1/2p_{n+1}},$$

$$(2) \qquad K_n = \frac{100(p_{n+1} - r_{n+1})}{1/2p_{n+1}},$$

where a prefixed s or d indicates that the following letter refers to the sire's or the dam's pedigree only, and $(p_{n+1} - r_{n+1})$ means the number of common ancestors for both pedigrees in the $n + 1$st generation.

As a measure of the proportion of the actual inbreeding due to relationship between the sire and dam of the individual Pearl has proposed to give a series of *partial inbreeding indices* calculated according to the formula

$$KZ_n = \frac{50(K_n)}{Z_n}.$$

[2] The values of F_{Tn} are given in Table I, "Studies on Inbreeding," VIII, 1917 (Pearl).

In this paper I wish to give a modification and some extensions to the method worked out by Pearl with the purpose of bringing all the measurements of inbreeding and relationship on the same scale and using total coefficients based on calculations of areas as the fundamental method in expressing degrees of kinship numerically.

I. Definition of the Coefficient of Relationship

If we plot the values of the coefficient of relationship obtained in accordance with the above indicated method together with the values of the corresponding coefficients of inbreeding for a given pedigree, we shall find that these corresponding values are not directly comparable as they are not worked out in relation to the same scale. To obtain this we need to change slightly the definition and formula of the coefficient of relationship.

Pearl's definition is the following: The coefficient of relationship indicates the number of ancestors common to both pedigrees of the two individuals whose relationship is being measured in proportion to the greatest possible number of *common* ancestors in this generation.

The proposed definition is this: The coefficient of relationship indicates the number of ancestors common to both pedigrees of the two individuals whose relationship is being measured in proportion to the total maximum number of *different* ancestors in the two pedigress taken together in the generation in question.

The formulæ are now the following:

(1) (When the relationship between the sire and dam of an inbred individual is being measured)

$$K_n = \frac{100(p_{n+1} - q_{n+1}) - ({}_sZ_{n-1} \cdot {}_sp_1 + {}_dZ_{n-1} \cdot {}_dp_n)}{p_{n+1}};$$

(2) (If any two different individuals are concerned)

$$K_n = \frac{100(p_{n+1} - r_{n+1})}{p_{n+1}}.$$

The difference between these formulæ and the first mentioned is only that the denominator in the fractions is multiplied by two. The total values, therefore, are exactly one half of Pearl's.

The maximum value of the coefficient of relationship will in every generation be 50, as no more than 50 per cent. of the individuals in a generation of a pedigree can appear in both halves of the pedigree.

II. The Total Relationship Coefficient

To measure the total degree of relationship during a number of generations I propose to use a total relationship coefficient based on the same common principles as the total inbreeding coefficient.

The areas to be compared are the area included by the relationship curve (corresponding to the inbreeding curve) and the area included by the maximum relationship curve. Now the maximum values of the coefficient of relationship are 50 in every generation beginning at K_1 and the area in question is for that reason simply 50 times the number of generations involved.

The formula of the total relationship coefficient for n generations is then the following:

$$K_{Tn} = \frac{100\Sigma^{Kn}_{Kl}}{50n} = \frac{2\Sigma^{Kn}_{Kl}}{n}.$$

III. Total Relationship Inbreeding Index

To indicate the proportion of the inbreeding that is due to relationship between the sire and dam of the individual, whose pedigree is being examined, I wish to propose a single numerical expression, the total relationship inbreeding index indicating the proportion of the area included by the relationship curve to the area included by the inbreeding curve, the formula being the following:

$$KZ_{Tn} = \frac{100\Sigma\frac{Kn}{Kl}}{\Sigma\frac{Zn}{Zl}}.$$

Calculation of the Coefficient Indicating the Degree of Inbreeding and Relationship in the Pedigree of the Jersey Bull King Melia Rioter 14th (103901)

To show the calculation and significance of the described coefficients I have selected the pedigree of King Melia Rioter Fourteenth including eleven generations. Table I gives the

TABLE I

$Z_1 = 25.00$	$K_1 = 25.00$
$Z_2 = 25.00$	$K_2 = 25.00$
$Z_3 = 37.50$	$K_3 = 31.25$
$Z_4 = 50.00$	$K_4 = 37.50$
$Z_5 = 71.88$	$K_5 = 43.75$

$Z_6 = 81.25$	$K_6 = 46.09$
$Z_7 = 90.63$	$K_7 = 46.48$
$Z_8 = 92.77$	$K_8 = 46.88$
$Z_9 = 93.65$	$K_9 = 46.88$
$Z_{10} = 93.85$	$K_{10} = 46.88$
Total 661.53	Total 395.71

values of the series of the coefficients of inbreeding and relationship for each generation.

The calculations of the total coefficients are now the following:

$$Z_{T_{10}} = \frac{100 \times 661.53}{900.10} = 73.50,$$

$$K_{T_{10}} = \frac{2 \times 395.71}{10} = 79.14,$$

$$KZ_{T_{10}} = \frac{100 \times 395.71}{661.53} = 59.82,$$

Or expressed verbally: In eleven generations King Melia Rioter Fourteenth is 73.50 per cent. inbred, his sire and dam are 79.14

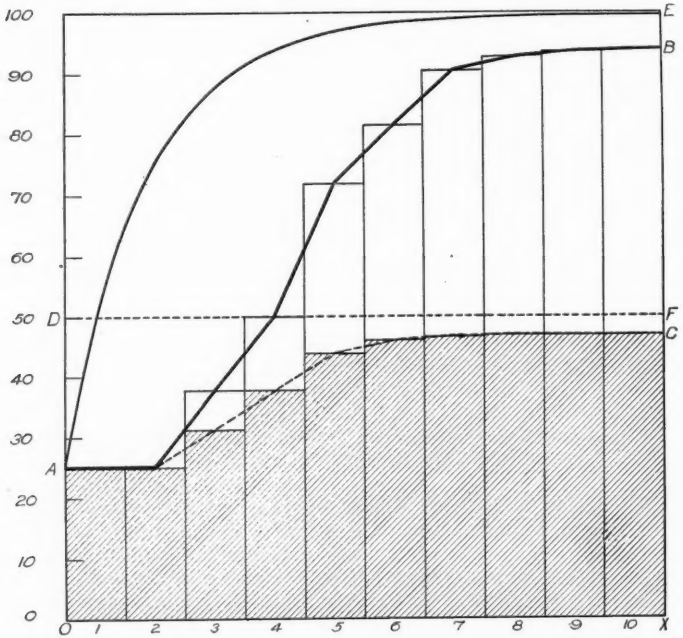

FIG. 1. For explanation see text.

per cent, related, and the part of the inbreeding due to relationship between his sire and dam is 59.82 per cent. of the actual total inbreeding.

In Fig. 1 the inbreeding curve and the relationship curve are plotted, based on the figures given in Table I, the former as a solid line, the latter as a broken line. The smooth curve indicates the maximum inbreeding curve; the broken line, that divides the area in two equal halves, indicates the maximum relationship curve. These four curves taken together give a fairly good graphical demonstration of the facts in question.

1. The area OABX in relation to the area OAEX gives the proportion of the actual to the maximum degree of inbreeding: *The total inbreeding coefficient.*

2. The area OACX in relation to the area ODFX indicates the proportion of the actual to the maximum degree of relationship: *The total relationship coefficient.*

3. The area OACX in relation to the area OABX gives the proportion of the inbreeding that is due to relationship: *The total relationship inbreeding index.*

In bringing all measurements of degrees of inbreeding and relationship to the same scale and using areas as the measures we get a uniform and significant series of coefficients that numerically express the degree of inbreeding and relationship in a given pedigree.

TAGE ELLINGER

COPENHAGEN.

SOME OBSERVATIONS CONCERNING THE PERIODICAL CICADA

DURING the recent visitation of the periodical cicada, their great abundance on the writer's home grounds at Vinson Station, Va., afforded an excellent opportunity to observe some of the habits of these interesting insects. During the months of January, February and March, the writer was engaged in clearing off all trees and brush from several lots immediately adjoining his home grounds. In the course of this work, several large oak trees were completely dug up by the roots. Even during the winter months, many of these benumbed creatures were encountered in their burrows in the soil around the roots. As warmer weather approached, their burrows became more numerous in the soil and it was evident that they were approaching the warmer, uppermost layer in ever-increasing numbers. Finally,

on May 18, the first adult was seen making its weak flight over my garden, having emerged some time during the previous night. A few evenings later the great exodus had begun in earnest and thousands of pupæ were issuing from the ground after sundown and ascending all the bushes, trees and posts in the vicinity to transform.

Although the actual exodus from the ground does not take place until after sundown each evening, the pupæ, in preparation for the event, excavate their burrows to the very surface of the ground and await the setting of the sun. In some instances the creatures burrow just to the surface, leaving a very thin layer of soil undisturbed over the exit. Frequently a tiny hole is punctured in the center of this thin surface layer. If these burrows are cautiously approached late in the afternoon long before sundown, the heads of the creatures may be seen near the surface. As the light intensity wanes with the oncoming of evening, the creatures come to the very surface, but quickly retreat if approached or disturbed. It is evident that the pupæ are negatively phototropic. If a pail or box is inverted over their burrows long before sundown so as to exclude the light, the creatures will shortly emerge as if night were really at hand. In this way I have brought many pupæ out of their burrows in broad daylight.

Although the pupæ quickly transform after emerging from the ground, it would be of interest to know just what conditions, external or internal, determine the impulse to prepare for the adult stage. If the creatures are prevented from leaving the ground or soil, the following experiments indicate that the pupæ will remain as such at least a day or two longer than when allowed to ascend trees and shrubs in the normal manner.

On the evening of May 24, five pupæ just emerging from the ground were captured and placed on the damp bare ground beneath a large inverted flowerpot, the drainage hole at the bottom of which had been closed. In addition to these, six other pupæ were captured and placed in a large flowerpot of similar size filled even to the top with loose soil. This pot was covered with a board. Both pots were examined next morning. The pupæ placed on the bare ground beneath the inverted, empty flowerpot were still crawling around, and none had transformed. Of the six placed in the pot containing soil, one had died. The remaining five were alive and active, and likewise none of these had transformed.

On May 25, the following experiment was made with these creatures. Early in the evening before the time had arrived when the creatures usually emerge in response to the low light intensity prevailing after sundown, many were captured by inverting boxes, etc., over the burrows. Later in the evening many more pupæ were captured as they were emerging from the ground in response to the normal darkness following sundown. Six were again placed on the damp earth beneath an empty, inverted flowerpot. Nine were placed as before in a full pot of soil, over which a board was placed to prevent their escape. As controls, six were placed on the branches of a shrub and kept under observation. One of the controls fell off and escaped. The remaining five soon transformed in the normal manner. The next morning, May 26, the pupæ kept beneath the empty, inverted pot and those in the soil were examined. Of the six placed on the bare soil beneath the empty, inverted pot, one had died but the rest were active. None had transformed. All nine pupæ placed in the pot containing soil were alive and crawling over the top of the soil. Likewise none of these had transformed. On the evening of May 26, three of these had died, but the remaining six were as lively as ever. These were then given their freedom and were allowed to crawl up into the branches of a small fringe tree nearby. One fell off and was lost, but the remaining five completed their transformations in the normal manner. Whether this temporary inhibition of the act of transformation is volitional or depends upon some factor of the soil environment acting upon them is not definitely established by these experiments.

After the pupæ ascend the shrubs and trees, rigidity sooner or later takes place, and the adult begins its emergence from the dorsal slit which opens in the pupal skin. It is not long until the lax, soft-bodied creature is hanging head downward by the tip of the abdomen. At this stage of its emergence, when it appears as if the helpless, soft-bodied creature must fall to the ground and perhaps suffer injury, it becomes very active, actually bending up to catch the exuvium or other near object with its legs, just before the tip of the abdomen is released. Not all pupæ are fortunate in their travels and transformations, however, for many come tumbling to the ground from the trees while they are making their way up the trunk and limbs. The almost helpless transformed adults also sometimes fail to secure a foothold and fall to the ground. It is interesting to note how quickly pigmen-

tation is completed after transformation. Immediately after emerging from the pupal shells, the adults are pale yellowish white, with two large conspicuous jet-black areas on the yellowish white prothorax. In a few hours the entire prothorax develops this same black pigment and becomes almost uniformly black.

In some localities the pupæ, in response to special conditions, construct neat little chimneys of earth several inches in height into which their burrows lead. I did not, however, find a single specimen of these unique structures in my locality, although the soil conditions varied greatly.

At Vinson Station, I was afforded an excellent opportunity to observe the occurrence, habits and notes of the dwarf or casinii form as well as the typical, much larger form, since both occurred here. Although the earliest musical expressions of the larger form were heard at my home on May 24, the distinctive notes of the dwarf form were not heard until nearly a week later. A rather well-defined colony of these smaller cicades appeared in some low, shrubby oaks only a few rods from my home, and remained locally abundant here throughout the period of their visitation. It was here that I spent much time in observing their habits. Although the pupæ of the larger and the dwarf form emerged from the ground within the same area in some places, and both forms were singing in the same trees and shrubs, both species appeared to mate among themselves. At no time did I observe a single instance of cross-mating. Although now and then I heard an occasional casinii form singing in the nearby woods, this form confined itself almost entirely to the narrow limits of the shrubby oak growths where it first appeared.

It now remains to consider the "songs" or musical notes of the larger and the smaller forms, for they are entirely different in character. The song of the larger form is a low, and to my ear usually pleasing, droning,—ah-oo—ah-oo—ah-oo—ah-oo—ah-oo. The first, or "ah" syllable is higher in tone and slurs down to the much lower pitch expressed by the syllable "oo." Each phrase "ah-oo" requires about five seconds, and the entire series may be prolonged for many seconds. During the act of "singing," the abdomen is noticeably raised toward the wings on every "ah" syllable, and is lowered on the lower-pitched "oo" syllable.

The "song" of the small Casinii form is a dry, lisping, tone-

less series of sounds, which to me seem best described by the syllables "it-see—it-see—it-see—it-see—it-see—it-see—see—see—see—see." The entire series of notes is hurriedly delivered and does not usually last over 8 to 10 seconds. The first notes of the series—"it-see—it-see "—usually begin slowly and are somewhat subdued in character. The syllables "it-see" gradually increase in loudness, and finally decrease somewhat in intensity, as they run into the shorter, more subduel syllables "see—see—see—see" which terminate the complete "song." The notes of this form are soft and lisping in character, and remind one of the noise of steam escaping intermittently, as one sometimes hears it around a locomotive.

During the height of the "song" season, one could rarely distinguish the notes of any individual, for the myriads of "voices" blended into a volume of soft, murmurous sound—a veritable atmosphere of sound which seemed everywhere to invest the trees and landscape from daybreak till darkness. It was a steady, droning, unceasing hum like the even whirr of machinery. The trees in the National Cemetery were fairly swarming with these creatures and their steady, murmurous chorus could be heard from morning until night, at a distance becoming softened and subdued, and reminding one of the soft murmurs heard when a big sea shell is held to one's ears.

Although the periodical cicada usually becomes silent after sundown, a great nocturnal chorus is sometimes initiated and a remarkable wave of sound invests the night for a time. On the night of May 31, I heard a most memorable, nocturnal chorus of this character, which began just before 2 A.M., solar time. One or two singers in the oak trees in my back yard initiated the concert. Others joined in, and there was a gradual swelling in the volume of sound until it seemed as if all the creatures in these trees were in full song. The concert did not stop here, for I heard it passing on to the big woods toward tulip poplar swamp, until the nighttime was fairly filled with murmurous sound. Gradually the crest of the wave passed outward into the more distant woods, while it subsided slowly in the trees in my back yard where the musical impulse appeared to originate. After some minutes all was quiet again around me, although I could just hear the great wave of sound receding or dying away in the distance. It was the most weird and remarkable chorus I have

ever heard. Hopkins describes a similar instance of this spectacular, nocturnal singing which he once heard.[1]

Many species of birds appeared to find these cicadas especially acceptable morsels. The blue birds in my boxes fed their young upon them extensively, as did a pair of song sparrows which had their nest in a pile of roots in my back yard. House wrens, English sparrows, red-headed woodpeckers and cuckoos fed upon them greedily. Some birds appeared frequently to snap them up in mere play as I once saw a cuckoo doing in the branches of a maple tree over my head. This bird snapped up first one then another in quick succession, quickly dropping them one by one, in a badly injured, helpless condition.

It is of interest to note that individuals differ in eye color. I have noted the following:

1. Males and females with red eye color.
2. Males and females with orange eye color.
3. Males and females with light buff eye color.
4. One male with noticeably white eye color. This individual was distinctive in other respects, since the large veins of the wings, markedly reddish in the common, red-eyed form, were pale yellowish in color. Red-eyed individuals predominate.

Some of the more important dates in the occurrences of the periodical cicada at Vinson Station I have recorded in my journal as follows:

May 18—First adult seen on the wing. The great exodus from the soil began during the next few days.

May 24—First "singing" of larger form heard. First singing of smaller Casinii form heard some days later, about May 27 to May 30.

May 30—Large form in copulation generally. First female noticed laying eggs in twigs.

June 5—Egg-laying activities at their height.

June 14—Creatures becoming very rare, and individual singers only occasionally heard.

June 20—All silent.

June 27—A single, belated individual of the larger form heard in "song."

Although the incessant concerts of the periodical cicadas persisting from morning until night became almost disquieting at

[1] See "The Periodical Cicada," by C. L. Marlatt, Bull. No. 14, Div. of Ent., U. S. Dept. of Agr., 1898, page 58.

times, I felt a positive sadness when I realized that the great visitation was over, and there was silence in the world again, and all were dead that had so recently lived and filled the world with noise and movement. It was almost a painful silence, and I could not but feel that I had lived to witness one of the great events of existence, comparable to the occurrence of a notable eclipse or the visitation of a great comet. Then again the event marked a definite period in my life, and I could not but wonder how changed would be my surroundings, my experiences, my attitude toward life, should I live to see them occur again seventeen years later.

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THE BEHAVIOR OF FUNDULUS HETEROCLITUS ON THE SALT MARSHES OF NEW JERSEY

During the year 1914–'15 the writer was retained as consulting zoologist to the department of entomology of the New Jersey Agricultural Experiment Station and engaged in studying the fish enemies of the salt marsh mosquitoes. At that time it became evident that *Fundulus heteroclitus* is the most important predatory fish attacking the salt marsh mosquitoes of northern waters. Much evidence of the efficiency of *Fundulus heteroclitus* as a mosquito exterminator has already been published (Chidester, 1916). Certain notes on its behavior under varied conditions have been amplified by more recent observations and are herewith presented in connection with the problem of migration in fishes.

In New Jersey the fish were studied under natural conditions for over a year on the salt marshes near the city of New Brunswick. Through the report system of the state inspectors of the Mosquito Commission, much important information was secured regarding conditions in other parts of the state. Experimental conditions were induced in the field by drainage ditches and in the laboratory by the use of aquaria. Other studies were made at Woods Hole, Mass., for several years during a portion of the month of June.

Material and Methods

On the salt marshes where the chief study was made there were numerous pools, some permanent, others easily differenti-

ated as temporary. The bottoms of the permanent pools were covered with soft mud and strewn with sedge and eel grass frequently dispersed in windrows as a result of repeated wave action. The bottoms of the temporary pools were covered with matted grass bound together by hardened clay.

At the Bonhamtown marshes near New Brunswick, intensive study was made of three large permanent pools, one of which was partially drained by a ditch connecting it with the Raritan River. Additional studies were made of conditions in many other permanent pools, temporary pools and ditches.

The three permanent pools studied most intensively were quite different in their character. The largest one was about 40 feet long and ranged from a foot to 10 feet in width, but its depth varied considerably with the tides. At its larger end it was connected with the Raritan River by means of a long narrow drainage ditch. The second was an almost circular pool about 25 feet in diameter and in no place more than 18 inches deep; much of the time it was only about 6 inches deep. The third pool was about 30 feet long and about 10 feet wide. At one end it was 20 inches in depth and at the other about 12 inches.

Collections were made by means of a 20-foot minnow seine and several small dip nets. Fish were frequently preserved in weak formalin in the field when it was desired to examine their stomachs at leisure. Usually, however, they were brought to the laboratory and examined freshly killed or else liberated in aquaria.

Records of temperature, salinity and specific gravity were taken with each collection, while the height of the tidal flow and the depth of the pools were approximately recorded.

SPRING MIGRATION

In the early spring, usually during the latter part of March, *Fundulus heteroclitus* begins its migration from the mouth of the Raritan River up beyond the salt water to the slightly brackish water of the salt marshes and even into fresh water creeks.

At first large numbers of medium-sized males appear, followed soon after by the medium-sized females (three or four years old) and later by the large and small of both sexes. By the middle of April great shoals of small fish crowd the streams and penetrate to the shallows. They seem undeterred by the sewage pollu-

tion of the river and are apparently impelled to seek out the farthest limits of tidal water.

Spawning takes place in April and continues until July in the region studied.

The factors influencing inland migration in the spring are several. The *temperature* of the inland waters which is at that time slightly higher than that of the ocean, and will later continue to increase, undoubtedly plays an important part. The fresh water teeming with life and the salt marshes with myriads of insect larvæ, shrimps, and young fish furnish *food* for the vigorous hungry fishes. The currents of fresh water have become stronger and as the fish needs must react to a stream of water not absolutely toxic to it, there is thus a *pressure stimulus* which powerfully attracts. Of perhaps less importance is the fact that the fresher waters when not too greatly contaminated by sewage pollution are *richer in oxygen.* Certain it is that many fish not anadromous come near the shore to spawn. Possibly the greater metabolism incident to the development of eggs and sperm causes them to seek out water which has a higher oxygen content. Roule (1914) believes that salmon migrate to a richer supply of oxygen. Wells (1915) has shown that starvation may cause certain fishes to seek water of lower concentration of salts and other species to behave in the opposite manner.

Summer Habits

During the summer until early August there is continual migration inland with the tides, many of the fish returning to the brackish water of rivers and creeks as the tide ebbs from the marshes. Some few individuals of the species *Fundulus heteroclitus* find sanctuary in the marsh pools, and in all probability so habituate themselves that they remain until cold weather. From the three permanent pools not partially drained by ditches, collections made during the year furnished the following species.

Number of Collections	Fundulus het.	Cyprinodon var.	Apeltes quad.	Anguilla
29	1,581	105	19	22

Since *Fundulus majalis* did not appear on the Bonhamtown marshes it was not feasible to repeat with that species the observations of Mast (1915), who found that it is not only prone to move with the tides, but that if the outlet to the ocean is plugged,

the fish will convey themselves overland by flopping in the general direction of the ocean. Mast shows that the fish are able to keep their sense of direction in the overland course and concludes that they remember the outlet. He believes that since there are apparently no external factors capable of guiding them, the behavior is dependent on internal factors.

Fundulus heteroclitus does not as a rule leap from pools, when left by the gradually receding tides. Two permanent pools were available for the study of the reactions of this species, one of them being connected with the Raritan River by a drainage ditch during the course of the study. This pool had been under continuous observation in an undrained condition and through an error workmen ran a drainage ditch to it, which did not, however, completely remove the water. After two days of the resultant condition the ditch was plugged with heavy sods and observations continued as before. The day after the ditch was plugged it was noted that there were many *F. heteroclitus* scattered all around the margin of the large oval pool. Although it was 25×15 ft., there was no marked variation in the distribution of the dead fish, except that there were none at the end farthest from the outlet. The banks were gently sloping and afforded an easy egress in any direction. The second pool with an outlet was long and narrow with high banks and was partially drained at the ebbing of the tide. When the receding water had left certain of the fish near the shallows at the exit, there was the usual attempt of the majority of fish to follow an outflowing current. But few individuals were caught in the mud, the majority returning to the deeper pool.

Since there is one predominant reaction in fishes, that to currents, it is quite probable that with *Fundulus heteroclitus* there is a less marked reaction to ebb tide. In the case of *Fundulus majalis* under natural conditions there must be an extremely rapid reaction to the condition of slack tide. Their disturbance under experimental conditions induced by Mast (1915), who plugged the entrance of the tide as it was coming in, indicates that this species does not normally accommodate itself to still water and that its stay inland is determined only by the tidal rise.

In the case of *Fundulus heteroclitus,* which migrates inland to the extremely shallow water covering the salt marshes at high tide, there is no such immediate response to receding water. The

fish return less quickly and seem to become readily acclimated to the still waters of permanent or even temporary pools to which they are directed as the tides recede.

In August there is a period of over two weeks when actively feeding killifish are almost completely absent from the marshes. That temperature plays a most important part in this behavior is indubitable. Shelford and Powers have shown (1915) that the herring is sensitive to temperature differences as small as 0.2° C. They have demonstrated that alkalinity and acidity are more important than salinity. The herring and salmon experimented with reacted to small fractions of a cubic centimeter per liter of H_2S and became negative to sea water which was slightly more acid than the fresh. It is possible that increased temperature may bring into solution organic substances which alter the alkalinity of the sea water or even render it acid near sources of pollution. Johnstone has shown (1908) that the migration of herring in Europe is closely associated with the salinity and temperature of the sea.

We may safely assume that *Fundulus heteroclitus* has an optimum temperature for its metabolism which will be higher when the animal is weak and poorly nourished, but lower when it is well fed. Thus a gradually increasing temperature while the animal is feeding will finally result in such warmth that normal metabolism is no longer possible and there will be no return to the fresher waters until they become cooler. Another factor of great importance in the inland movements of *Fundulus* is the fact that after spawning, the animals are sluggish and hence in no condition for a battle with the tides. This factor is probably the one that causes almost complete disappearance of the larger and the medium-sized *Fundulus* during August in the area studied.

Fall Migration

Early in September large numbers of *Fundulus heteroclitus* of small and medium size return to the marshes with the tides, and they continue to run in and out until the water becomes extremely cold. There are fewer individuals remaining in the pools between tides, but many are still found variously dispersed among temporary pools far inland.

Their food is somewhat reduced so far as mosquito larvæ are concerned, but there are many other insects available, besides small eggs and shrimps.

WINTER HABITS

The habits of *Fundulus heteroclitus* in the ocean in winter are not fully known. The late Vinal Edwards of the U. S. Bureau of Fisheries, Woods Hole, Mass., stated to the writer that it was his observation that they spend a large part of the winter near the mouths of rivers in water which is moving and which is at a salinity slightly lower than that of the sea.

In November, when the temperature of the water on the marshes goes down to 40° F., the migration inland is much reduced. Field observations showed that fish in temporary pools at this time attempted to burrow in the bottoms and being of course unsuccessful on account of the hardness of the clay died during the night as the temperature went down to nearly the freezing point. In the case of permanent pools whose bottoms were covered with soft mud, the fish burrowed down during the night and emerged when the sun came out and warmed the water.

At about the time that ice begins to form over the permanent pools, migration ceases so far as the marshes are concerned. In the pools, fish were found burrowed in the mud at a depth of from 6 to 8 inches in the middle of the winter. The temperature of the mud was from 40° F. to 45° F. and that of the water ranged from 32° F. to above 40° F., even in February, since the shallower pools were warmed considerably by the sun. On bright days when the sun was most effective, a few hardy fish ventured forth from hibernation and swam slowly around under the ice, feeding but little. Associated with them were shrimps, myriapods, eels and another minnow (*Cyprinodon* var.), all of which were burrowed in the mud during most of the winter.

Examinations of the stomach contents of *Fundulus* showed that the food during the winter was largely algal matter in those individuals that became active. By far the majority of the fish remained torpid until early spring, beginning to feed again in March, and reassuming complete activity early in April.

SUMMARY

1. Field studies of *Fundulus heteroclitus* were made throughout one entire year on the salt marshes of New Jersey.

2. Spring migration begins in March and is probably caused by several factors, including the higher temperature of the inland water; currents due to high tides and rainfall; the need

for food available in fresh water; greater metabolic activity due to gonad development which demands a greater oxygen supply.

3. Summer activities consist in spawning, feeding, lazy movements from the marshes to the brackish water and back again.

4. In the autumn, migration is less constant and the larger fish are less numerous.

5. In the winter, migration ceases entirely as the marsh pools are scumming with ice. Some landlocked individuals burrow into the mud of permanent pools, coming out occasionally as the sun warms the water. Many fish are killed by the cold as they remain in temporary pools with bottoms composed of caked mud and grass offering no shelter.

6. The majority of *Fundulus heteroclitus* return to salt water in the winter, probably remaining near the mouths of rivers until spring.

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INDEX

NAMES OF CONTRIBUTORS ARE PRINTED IN SMALL CAPITALS

AGERSBORG, H. P. K., Utilization of Echinoderms and Gasteropod Mollusks, 414
Alkalinity of Sea Water, W. J. CROZIER, 88
ALLARD, H. A., Periodical Cicada, 545
Amicronucleate Race of *Paramecium caudatum*, EUGENE M. LANDIS, 453
Animal Life and Sewage, FRANK COLLINS BAKER, 152
Assortative Pairing in *Chromodoris*, W. J. CROZIER, 182

BABCOCK, ERNEST B., *Crepis* and Genetic Investigations, 270
BAKER, FRANK COLLINS, Animal Life and Sewage, 152
BARBOUR, THOMAS, A Recent Check-list, 284
Behavior of *Fundulus heteroclitus*, F. E. CHIDESTER, 551
Bionomics, of *Porichthys notatus* Girard, 380; of *Mellita*, W. J. CROZIER, 435
BRUES, CHARLES T., Plants and Insects, 313

Congenital, Palsy in Guinea-pigs, LEON J. COLE, 130; Cataract in Cattle, J. A. DETLEFSON and W. W. YAPP, 277
CASTLE, W. E., Whitman and Castle on Orthogenetic Evolution in Pigeons, 188
Check-list, THOMAS BARBOUR, 284
Chiasmatype and Crossing-over, E. B. WILSON, T. H. MORGAN, 193
CHIDESTER, F. E., Behavior of *Fundulus heteroclitus*, 551
Chitons, Coloration, 84; Photic Sensitivity of, W. J. CROZIER, 376
COLE, LEON J., Congenital Palsy in Guinea-pigs, 130
Color Classes, Exceptional, in Doves and Canaries, C. C. LITTLE, 162
Crepis and Genetic Investigations, ERNEST B. BABCOCK, 270
CROZIER, W. J., Sex-correlated Correlation in *Chiton tuberculatus*, 84; Alkalinity of Seawater, 88; Assortative Pairing, 182; Photic Sensitivity of the Chitons, 376; Bionomics of *Mellita*, 435

DAVENPORT, C. B., Human Twins, 122
DETLEFSON, J. A., and W. W. YAPP, Congenital Cataract in Cattle, 277
DUERDEN, J. E., The Callosities of the Ostrich, 289
DUNN, L. C., Sable Varieties of Mice, 247; White-spotting in Mice, 456

EAST, E. M., Hybridization and Evolution, 262
Echinoderms and Gasteropod Mollusks, H. P. KJERSKOG-AGERSBORG, 414
ETTINGER, TAGE, Numeral Expression of the Degree of Inbreeding, 540
Evolutionary Aspects of Human Mortality Rates, RAYMOND PEARL, 5

Factorial Values, C. ZELENY, 358
Fossilization of Blood Corpuscles, ROY L. MOODIE, 460

GRIFFITH, COLEMAN R., Bodily Rotation and the White Rat, 542

Habitat Responses, C. F. CURTIS RILEY, 68
HADLEY, PHILIP, Trichomonas and Blackhead in Turkeys, 176
Hair of Mammals, LEON A. HAUSMAN, 496
HARVEY, E. NEWTON, Regulation in Plants, 362
HAUSMAN, LEON A., The Free-swimming Mastigophora, 333; Vibratile Membranes of *Glaucoma scintillans*, 427; Hair of Mammals, 496
HAGEDOORN, A. L., and A. C. HAGEDOORN-LABRAND, White Rat and Bacterial Diseases, 368
Heredity, H. J. MULLER, 97
HUBBS, CARL L., Bionomics of *Porichythys notatus* Girard, 380
Hybridization and Evolution, E. M. EAST, 262

IBSEN, HERMAN I., Linkage, 61
Inbreeding in Maize, Intolerance of, PAUL WEATHERWAX, 184
Individuality-Differential and its Inheritance, LEO LOEB, 55
Inheritance of Congenital Palsy in Guinea-pigs, LEON J. COLE, 130
Inherited Predisposition for a Bacterial Disease, A. C. HAGEDOORN, LABRAND and A. L. HAGEDOORN, 368
Insect Enemies of Polyporoid Fungi, HARRY B. WEISS, 443

JACOBS, M. H., Rate of Respiration in Small Organisms, 91

LANDIS, EUGENE M., Amicronucleate Race of *Paramecium caudatum*, 453
Linkage in Rats, HERMAN I. IBSEN, 61; Measurement of, C. C. LITTLE, 264
LIPPINCOTT, WILLIAM A., Pelvic Wing in Poultry, 536
LITTLE, C. C., Exceptional Color Classes in Doves and Canaries, 162; Linkage, 264
LOEB, LEO, Tissues and Degrees of Family Relationships, 45; Individuality-Differential and its Mode of Inheritance, 55

MAGATH, THOMAS BYRD, The Nematode Genus *Camallanus*, 448
MOODIE, ROY L., Fossilization of Blood Corpuscles, 460
MORGAN, T. H., Secondary Sexual Characters of the Fiddler Crab, 220; and E. B. WILSON, Chiasmatype Crossing-over, 193
Mortality Rates, Human, RAYMOND PEARL, 5
MULLER, H. J., Heredity, 97

Nastigophora, the Free-swimming, LEON A. HAUSMAN, 333
Nematode Genus, *Camallanus*, THOMAS BYRD MAGATH, 448
Neotony and the Sexual Problem, W. W. SWINGLE, 349
Numeral Expression of the Degree of Inbreeding, TAGE ETTINGER, 540

Ostrich, Inheritance of the Callosities of, J. E. DUERDEN, 289

PEARL, RAYMOND, Evolutionary Aspects of Human Mortality Rats, 5
Pelvic Wing in Poultry, WILLIAM A. LIPPINCOTT, 536
Periodical Cicada, H. A. ALLARD, 545

RAYMOND, PERCY E., Phylogeny of the Arthropoda, 398
Regulation in Plants, E. NEWTON HARVEY, 362
Relationships, Family, Tissues and Degrees of, LEO LOEB, 45
RILEY, C. F. CURTIS, Habitat Responses, 68
Respiration, Measuring rate of, M. H. JACOBS, 91
Rotation, Continued Bodily, of White Rat, COLEMAN R. GRIFFITH, 542

Sable Varieties of Mice, L. C. DUNN, 247
Secondary Sexual Characters of the Fiddler Crab, T. H. MORGAN, 220
Selection of Food Plants by Insects, CHARLES T. BRUES, 313
SETCHELL, WILLIAM ALBERT, Stenothermy and Zone Invasion, 385
Sex in *Mercurialis annua*, CECIL YAMPOLSKY, 280
Sex-linked Lethal Factor in Mammals, C. C. LITTLE, 457
SWINGLE, W. W., Neotony and the Sexual Problem, 349

Trichomonas and Blackhead in Turkeys, PHILIP HADLEY, 176
Twins, Human, Production of, C. B. DAVENPORT, 122

Vibratile Membranes of *Glaucoma scintillans*, LEON A. HAUSMAN, 427

WEATHERWAX, PAUL, Intolerance of Inbreeding in Maize, 184
WEISS, HARRY B., Insect Enemies of Polyporoid Fungi, 443
White-spotting in Mice, L. C. DUNN, 456
Whitman and Riddle, Evolution in Pigeons, W. E. CASTLE, 188
WILSON, E. B., and T. H. MORGAN, Chiasmatype and Crossing-over, 193

YAMPOLSKY, CECIL, Sex in *Mercurialis annua*, 280

ZELENY, C., Factorial Values, 358
Zone Invasion and Stenothermy, WILLIAM ALBERT SETCHELL, 385